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PART 2

TRANSACTIONS

OF THE

SOCIETY FOR BRITISH ENTOMOLOGY

EDITED BY
J. H. MURGATROYD, F.L.S., F.R.M.S., F.Z.S.

WITH THE ASSISTANCE OF
W. A. F. BALFOUR-BROWNE, M.A., F.R.S.E., F.L.S.,
F.Z.S., F.R.E.S., F.S.B.E.
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G. J. KERRICH, M.A., F.L.S., F.R.E.S.
O. W. RICHARDS, M.A., D.Sc., F.R.E.S., F.S.B.E.
W. H. T. TAMS

Date of Publication: 31st July, 1950

Copies may be purchased from the Secretary at 454 Christchurch Road, Bournemouth, Hants

Price 10s. 0d., post free

Price 10/- Subscribers
Published by Council
Feb. 2nd. 1952

U.S. DEPT. INST.
U.S. NATL. MUS.

SOCIETY FOR BRITISH ENTOMOLOGY

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TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 10 JULY 31ST, 1950 PART 2

AN INTRODUCTION TO THE NATURAL HISTORY OF BRITISH SAWFLIES

(*Hymenoptera Symphyta*)

By

ROBERT B. BENSON, M.A., F.R.E.S., MEM. HON. S.E. BELG.

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1. INTRODUCTION

(*a*) General

The need for an up-to-date systematic work on the British Sawflies will be apparent to anyone who has tried to name material with the existing literature; and it has for long been one of my immediate ambitions to supply this need. This ambition is now within sight of realization; and the Synopsis will soon appear in the series of Handbooks for the Identification of British Insects, Vol. VI, produced by the Royal Entomological Society of London. To that work the reader is referred for the determination and classification of his material.

In writing the handbook very little about the general biology of sawflies could be included; as, however, a summary of the information so far collected might prove interesting and useful to others it has seemed worth while writing this Introduction to the Natural History of British Sawflies as a companion to the systematic paper. And now I hope that these two papers together will stimulate a wider interest in these insects.

Actually the present paper was first written up in 1941-2; publication has, however, been delayed so that the nomenclature should be in conformity with the still unfinished systematic work. Since that time it has been brought up to date from information that has come to hand in the ordinary course of events but no further special search of the literature has been attempted. Both Dr. B. M. Hobby and Mr. G. J. Kerrich kindly read through the manuscript for me and made useful suggestions.

(*b*) The Previous Systematic Framework

In Cameron's work (1882-1892) the keys to systematic categories are extremely difficult and often impossible to use. Although this monograph is still a source of information on the biology and general morphology of sawflies, much of this is inaccessible or misleading without interpretation, as many of the species dealt with are now, for various reasons, known by other names.

Morice (1903-1916) attempted to revise the sawflies known to him, largely on the basis of the published works of Konow and Enslin on the central European sawflies. His keys were more practical than Cameron's and although he added several good species to our lists the total number of British species was reduced from 374 to 346, of which only 321 are now considered valid. This reduction was justified in many cases, but in others was retrograde, and resulted from relying too much on the synonymical guesses of Konow and Enslin, who attempted to dispose of all the Cameron species that they had never seen, as synonyms of any well-known or common species in the same genera. Morice often made no

attempt to examine the Cameron types in the British Museum himself and form his own conclusions. The standard work on central European sawflies is that of Enslin (1914-1918).

From 1916 and until his death in 1925 Morice was engaged in rewriting his "Help Notes" so that they could be published in book form. Primarily to help him in some of the more difficult genera, Dr. R. C. L. Perkins, F.R.S., started working on the British sawflies in Devonshire and added many species to our lists, bringing the total up to 388 (1929). He worked specially on the Nematinae and *Dolerus*; he prepared keys to most of the genera of Nematinae, and his key to *Dolerus* was ultimately published (Perkins, 1930). He kindly allowed me to take copies of his keys to the Nematine genera. These have been extremely useful in the past, but are now altered beyond recognition to accommodate the more recent additions to our fauna. At the present time the British total stands at round about 460 native or established alien species.

The actual number of known British species will undoubtedly be further increased as time goes on, especially if their early stages are studied more. Additions to the British Sawfly fauna will as a general rule be referred to in current numbers of the Entomologist's Monthly Magazine.

At the time of Morice's death in 1925 the revision of his Help Notes was still incomplete and not in any form that could be published; in my recent synopsis scarcely any use has been made of it. I am indebted to the late Sir E. B. Poulton, F.R.S., and Professor G. D. Hale Carpenter, D.M., M.B.E., for allowing me access to this manuscript and for the loan of the Morice and part of the Perkins Sawfly collections, now presented to the Hope Department of Entomology, Oxford University Museum. These specimens have been most useful to me for comparative purposes during the laborious recent years when I have been building up a representative collection of British sawflies at the British Museum, sufficient for an attempt to be made at a systematic synopsis. Without the help of these specimens my work would have been even still more difficult. I also owe a deep debt for help and encouragement to Dr. R. C. L. Perkins, F.R.S., and his son, my colleague, J. F. Perkins.

For information on Irish sawflies I am much indebted to Mr. A. W. Stelfox, A.L.S., of the Dublin Museum and Mr. R. C. Faris of Cavan.

2. FIELD AND COLLECTING NOTES

(*a*) General

Sawflies are on the wing mostly in the spring and early summer. *Dolerus*, *Amauronematus* and *Aglaostigma* (Tenthredinidae) begin to

appear in the south of England on warm sunny days in March. The peak of the season for the Tenthredinid Nematinae and other spring sawflies is usually in May in the south of England and June in Scotland. Certain Argidae and Tenthredininae predominate in July, and in August appear second broods of certain of the early species. *Apethymus abdominalis* Lep. (Tenthr. Blennocampinae) is on the wing only in September and October; this species, *A. braccatus* Gmelin and *Neodiprion sertifer* Geoffroy (Diprionidae) are exceptional in passing the winter in the egg stage; the species of *Dolerus* (Tenthr. Selandriinae) winter as pupae; the Siricidae as feeding larvae, prepupae or even adults; all other species, so far as is known, pass the winter as fully-fed hibernating larvae (prepupae). Except in those three species that winter as eggs, the larvae, whether feeding exposed, in galls, mines or leaf-rolls, should be looked for from two to three weeks after the flight of the adults. Mostly they then feed up in a few weeks, but *Tenthredopsis* (Tenthredininae) and other low-feeding larvae found feeding very late in the year mature slowly, so that those found in December have probably been feeding for at least three months. *Urocerus gigas* L. and other wood-borers may spend three or more years as feeding larvae.

As soon as the larva is fully-fed, it usually casts its skin, either before or after preparing a hibernaculum, and passes into the prepupal resting stage in which it survives the rest of the summer, autumn and winter. The prepupa is much like a larva in form, but it does not feed; and its colour pattern, spines, hairs, etc., are very much reduced. In *Amauronematus* (Tenthr. Nematinae), which is single brooded, larvae are sometimes fully-fed by the end of May and survive all through the summer until at least the following March as resting prepupae. Not all the larvae of a brood will necessarily become adults in the same season. For example, from a single brood I had under observation of *Hemichroa crocea* Geoffroy (Tenthr. Nematinae) larvae feeding in midsummer from spring adults, some produced flies in August; others remained over the winter as prepupae and emerged as flies in the following June; and a few others till the August following that. In *Gilpinia hercyniae* Htg. (Diprionidae) some individuals pass as many as six winters in a resting state before emerging as adults (Prebble 1941).

The adults on the wing are rather short-lived. In captivity it is difficult to keep males of the smaller species alive more than 3 or 4 days or females more than 7 to 14 days, but the actual flight of a species may be spread over weeks or months, the males generally appearing first. Fluctuations in the numbers of a species may be great from year to year; remember therefore that if you should come on a species in abundance such an opportunity may never occur to you again.

(*b*) Foodplants

Because most sawflies are very specialized in their choice of foodplant and are weak fliers, a knowledge of their foodplants is of primary importance in collecting. A few British species are polyphagous, but most are highly specialized, many attacking only one part of a single plant-species. Furthermore it should be remembered that apparent polyphagy often hides a subdivision of the species into highly specialized foodplant races, perhaps further incipient species (see Section 5 (*d*) (i), "Foodplant Races").

More than half the British sawflies whose hostplants are known (including most of the Tenthredinid Nematinae) are attached to woody plants: over 100 to the Salicaceae (*Populus* and especially *Salix* with more sawflies than any other plant, each species or species group of which has its own special sawflies); the Betulaceae about 60 (*Betula* and *Alnus*); the Rosaceae about 80 (various shrubs and herbs); the Coniferae over 30 (*Pinus*, *Picea* and *Larix* about 12 each); Gramineae and Juncaceae, taken together, over 30; *Quercus* 16; *Equisetum* with 10 (all of them Dolerini).

In addition to these many other plant orders are attacked by one or two species only.

A large proportion of British sawflies are in fact attached to anemophilous flowering plants and, next to these, come simple entomophilous plants with a prolific pollen production, and ferns with their prolific spores. From what little is known, the same general rule may well apply to the world species; but the ferns would probably appear as an important foodplant, for such groups as the abundant Tenthredininae and the Strombocerini of the Selandriinae seem to be largely associated with ferns.

(Further discussions on foodplants can be found under 4 (*c*) Ecology and Biogeography, 4 (*g*) Ecological Origins of Sawfly Groups, and 5 (*d*) (i) Foodplant races, while the symbiosis occurring in Siricidae and Xiphydriidae is dealt with in 3 (*c*) Symbiosis between Fungi and Wood-borers. A complete foodplant list of British sawflies arranged under plant families is included in the Systematic Handbook.)

(*c*) Habitats

From the above it can be seen that the most productive localities will be the edges of rivers or still water, marshes, swamps, fens, bogs, damp heathland, open and scrubby woodland and coniferous plantations or forest. Gardens and rich flowery hedgerows, pastures or downlands are also good. Avoid game reserves, which are generally poor, and seek out regions such as relic forest or bog—osier beds are often rich. Very small such areas are often good and seem comparatively richer than larger unspoilt areas, as species are often concentrated here as if they had been driven out from the

surrounding country. Patches of relic arctic plants in northern districts should be specially worked, as in arctic regions there is a rich sawfly fauna. Several such species are only known in Britain from the summits of the highest mountains.

(See also the various chapters under 4 Distribution.)

(*d*) Collecting

Collecting in the spring is most profitable on still, sunny days. With practice sawflies can be recognized on the wing; it is best to face the sun and shade the eyes above; they then appear silvery in flight and fly steadily and slowly, not swerving rapidly as do many hymenoptera with petiolate abdomens. They are also fond of alighting and crawling on leaf-surfaces exposed to the sun, and to watch for this it is best to face away from the sun. Many species feed on pollen and some, especially Tenthredininae, Blennocampinae and Argidae, visit such flowers as Umbelliferae where nectar is easy to obtain, or where they can catch other insects as prey or find their mates so doing. Others should be looked for on their foodplants; the females of many species can be swept from the opening buds or young leaves of their foodplants, as can the males hovering above them.

The spring Nematinae attached to *Salix* favour the catkins of these shrubs; the species of *Hoplocampa* should be sought from the blossoms they oviposit in. General sweeping will produce the species attached to low plants, and under trees particularly those newly emerged or at rest from those trees.

In collecting it is essential to remember that sawflies are very sensitive to weather conditions, such as temperature, humidity and wind; and that many of them are not strong fliers and hide away if these conditions are unsuitable. In summer when the days get very hot the sawflies will tend to hide away in the middle of the day and must be looked for in the late afternoon and evening (the early morning is usually too wet with dew). It is useless trying to collect in exposed places in a high wind, though sheltered hollows are then often very profitable. On dull warm days, even sometimes when rain is falling, beating and sweeping are profitable as long as the vegetation is dry enough.

Species whose larvae live in galls or leaf-mines, or that live in conspicuous communities, or make characteristic scars in the leaves, are often much more easy to find as larvae than adults, and are easier obtained thus by breeding. Some low-feeding larvae, such as many Tenthredininae, are seldom seen, being mostly nocturnal, coming out to feed only at night or when the air is very humid in the daytime.

If any sawflies are brought home alive, never more than one

should be put in each tube or box; if two or more are kept in a confined space for long they are likely to bite off each other's legs and antennae, so that the males are unable to hold the females for copulating and the females are unable to get a firm stand for ovipositing. The females of most sawflies will oviposit readily even if they have no access to a male. Their parthenogenetic offspring may be entirely male, mixed or entirely female according to species, race or climate. (See Section 5 (*c*).)

For guidance on collecting material the new edition of the British Museum collectors' handbook on Insects should be consulted (Smart, 1940).

(*e*) Mounting

Small sawflies should be pinned on minute stainless steel pins which are pushed into polyporus strips and staged on large cabinet pins; bigger insects can be pinned on large stainless steel pins. The insects are easiest to examine and compare with each other if they are all set uniformly with wings spread as in Lepidoptera, but, if this is not done, the wings should at least be moved so that they do not dry over the abdomen, which must be visible from above, and separated from each other so that the venation of the hind-wing can be seen without difficulty.

If the insect is staged on polyporus or card it should not rest actually on the stage, but be raised some distance above it so that the underside of the specimen is visible. Some of the legs should also be spread out so that the underside of the thorax can be examined easily as well as the different segments of the legs, claws, etc. To protect the very fragile antennae of Nematinae a good plan would be to place a minute spot of seccotine at the junction between the flagellum and the second antennal segment, as it is at this point that the antennae so often break off in dried specimens. It is well to open the mouth parts as much as possible (the insects will do this of their own accord if subjected to ethyl acetate fumes before killing), to straighten the antennae and legs so that they can be measured easily, gently to squeeze out the genitalia if the specimen is a male, or press out the saw so that it projects beneath the sheath if a female—this is best done by pressure each side of the hypopygium with fine-pointed forceps—though great care must be taken not to damage or disarrange the sawsheath valves. If these things are done it will often be possible to examine the mouth parts, genitalia, etc., without mounting them on slides, and if it is decided to make microscopic slides these parts can much more easily be detached. An alternative method of mounting is to gum the insects on their sides on card, one pair of wings being fixed down and the other pair left free. This method has certain advantages in that the insect is better protected, and that the under-

side can be seen as well as the upperside without turning the pin upside down, but if this method is adopted care must be taken not to clog the face, claws and genitalia with gum and for this reason one hind leg should be left free. The technique of this method has been perfected by Mr. A. W. Stelfox and has been adopted by others owing to their present difficulty in getting pins, but the method deserves wider applicability, so long as all the above details are attended to. Sawflies should *never* be gummed down flat on card or celluloid in the old style as many important characters are thus rendered invisible.

When sawflies cannot be mounted at once, such as during collecting trips, they should be spread out thinly between layers of cellulose wool (which will not catch in their claws) and packed in boxes or butterfly envelopes; and they then can easily be relaxed later for mounting at leisure. If they are to be packed in tins it is very important not to pack them tightly at first, as there is great danger from mould if they are not dried. It is important to remember that a few specimens in perfect condition are always to be preferred to large quantities of imperfect specimens; nevertheless, long series are desirable. In the later systematic studies one can never have too much material in good condition: supposed common species in the field often turn out to be a mixture of several species including perhaps a new one occurring as a very small percentage of the whole; or a mere sample of a supposed common species taken in a special locality may turn out to be a new one or a new local race difficult to define with certainty because of the smallness of the sample.

(*f*) Labelling and Recording

Great care should be spent in labelling the specimens, preferably including the Watsonian vice-county number on the label; the whereabouts of small villages, woods or hills being indicated by a mention of the parish they belong to and their nearest large town in the same county. All specimens correlated with biological observations should be carefully preserved *however bad their condition.* This is important, as, with the increase of knowledge, species will be further split or differently divided and then actual bred specimens will be needed for correlating biological information.

In publishing records of plants or animals, the mere name is often insufficient; it is very often important, and therefore always wisest, to indicate either who named the specimen and when, if he is a specialist, or what books were used in so doing if not named by a specialist, because names are often used in different senses by different workers or by one worker at different times. Parasites should always be carefully labelled and kept for reference. Adequate samples of foodplants may often prove important in any case of

doubt and are an essential accompaniment of *Salix* galls from which *Nematus* (*Pontania*) (Nematinae) have been bred.

3. BIOLOGY

(*a*) Eggs

Sawfly eggs are of the usual insect type and are mostly elongate-oval, kidney-, sausage- or cigar-shaped. Xiphydriidae and Orussidae are remarkable in having eggs with a long curved stalk as in the Cynipoidea and Chalcidoidea. Others, such as *Cephalcia* (Pamphiliidae) have an umbilical shaped knob on the convex side. The eggs are entirely or at least partly (e.g. by the umbilical shaped knob in Pamphiliidae) embedded in the tissues of their foodplants and are usually deposited singly, one to each pocket or slit cut by the saws, though there may be many pockets to a leaf or stalk. In Siricidae, however, there is usually more than one egg in each oviposition channel, 3 to 4 is quite a common number and 6 is recorded (Chrystal, 1928). The oviposition habit is naturally closely correlated with the form of the saw.

The size and shape of the egg is often specific. Forsius (1920) gives the sizes and colours of the eggs of 124 European sawflies; the smallest known egg according to Forsius is 0.35×0.15 mm. (*Fenusa dohrni* Tischbein (Tenthr., Blennocampinae)) and the largest is 3.90×0.92 mm. (*Acantholyda posticalis* Matsumura (=*pinivora* Enslin) (Pamphiliidae)). The number of eggs laid varies greatly between genera but averages about 60. Scheidter found as many as 1,000 eggs in a dissected female of *Urocerus augur* Kl. (Siricidae) while *Acantholyda erythrocephala* L., according to Forsius, lays only about 16. There is, however, usually a discrepancy between the number of eggs produced and those actually laid in captivity.

The size of the egg increases with the growth of the embryo, as is usual. For example, eggs of *Strongylogaster mixta* Klug (Tenthr., Selandriinae), which when first laid were 0.88 to 0.94×0.36 to 0.38 mm., increased after four days to 1.0×0.45 mm. and after eight days to 1.25×0.60 mm. according to Forsius. This growth of the egg leads to a pushing out of the surrounding tissues, which are thus swollen as if by a gall.

Except in species that overwinter as eggs (*Apethymus* spp. (Tenthr., Blennocampinae) and *Neodiprion sertifer* Geoffroy (Diprionidae)) the larvae hatch generally in from 9 to 14 days after the eggs are laid. Chrystal (1928) estimates 3 to 4 weeks in Siricidae, Gösswald (1935) up to 40 days for *Diprion pini* L. (Diprionidae), while a minimum of 3 days has been recorded for the Tenthredinidae, *Protemphytus tener* Kl. (Vasiliev 1925), *Rhadinoceraea micans* Kl. (Polizu 1935) and *Pristiphora abietina* Christ. (Nägeli 1936). The length of incubation will vary enormously in the same species

according to temperature, humidity, etc.; for example, it varies in *Hoplocampa flava* L. (Tenthr., Nematinae) from 4 to 24 days (Miles, Thomas and Hey 1933).

Generally the eggs are very sensitive and are easily killed by excessive damp, cold, heat or drought, but overwintering eggs have survived as low temperatures as —30° C. (Forsius). Bodenheimer (1932) showed that, in the Cimbicid *Cimbex quadrimaculata* Müller, there was a very high egg mortality in Palestine through deficiency of moisture; in fact the optimum relative humidity of this (and ? most) species is about 100%.

(*b*) Larvae and General Biology

The study of life-histories is a vast subject which can scarcely be touched on here, except in so far as it will help the beginner in collecting and rearing. The amateur has here the chance of discovering useful knowledge, knowledge that is becoming more and more essential in separating species and in being ready to deal with pests.

A vast field remains to be explored in such subjects as oviposition habits, temperature and humidity requirements, and parthenogenesis. Much has been discovered in the last few years as a result of investigations carried out on the Canadian spruce sawfly (*Gilpinia hercyniae* Htg.), introduced from Europe. The papers by Balch, Prebble, Gobeil and Smith, referred to below, are well worth study by the student.

From June until late autumn larvae can be found in abundance. The majority are free feeders on leaves, being either social and conspicuous, or solitary and inconspicuous. Inconspicuousness is achieved by the larvae resembling leaves in colour and their clinging close to the leaves when feeding, or by their feeding only on the undersides of leaves, or by their only coming out to feed in wet weather or after dark, hiding away at other times; though the actual cause of these secretive habits is probably sometimes their high humidity requirements. In the field, leaves damaged by larvae are usually the first clue to their presence. Some eat out round holes in the leaves, others feed only on the edges, or only the upper surface (or lower surface) of the leaf (most edge-feeders start by making holes or by feeding only on the surface). Some live in blister leaf-mines between the upper and lower epidermis (Heterarthrinae, Fenusini of Blennocampinae, and *Pseudodineura* of Nematinae).

Several, including some of the most primitive families, bore in stems, twigs or wood (all the Cephidae, Blasticotomidae, Xiphydriidae and Siricidae as well as *Ardis*, *Dolerus cothurnatus* Lep. and *Eutomostethus luteiventris* Kl. of Tenthredinidae).

A few live in rolled leaf-edges or rolled leaves (*Nematus* (*Pontania*) spp. (Tenthr., Nematinae) on *Salix*, *Blennocampa pusilla* Kl.

(Tenthr. Blennocampinae) on *Rosa*, *Pamphilius* spp. (Pamphiliidae) on various trees), or in communal webs (*Neurotoma saltuum. L.* (Pamphiliidae) on rosaceous shrubs), while yet others live in catkins (*Xyela* (Xyelidae) in *Pinus*, *Amauronematus amentorum* Förster (Tenthr. Nematinae) in *Salix*) or the fruits of rosaceous trees and shrubs (*Hoplocampa* of Tenthr. Nematinae), or in galls (*Nematus* spp. (Tenthr. Nematinae) in *Salix* stems or leaf-veins, or in bean- or pea-galls on *Salix* leaves).

Full-fed larvae generally change into prepupae (with different pattern to the larvae) and leave their foodplants to form a cell or cocoon in which to pupate after a resting period. The site chosen may be in the soil (in Pamphiliidae up to a depth of six or eight inches), among debris, in soft wood or bark, or in twigs and stems (not necessarily belonging to their foodplant), in galls of other insects, in apples on the ground, or even exposed on the branches of their foodplant. In species, especially Nematinae, with more than one annual brood the summer cocoons are often spun among the leaves of the foodplant and only the overwintering generations spin their cocoons underground.

Owing to their very thin cuticle many larvae and pupae are very sensitive to moisture deficiencies. In many Nematinae, for example, it has been found that unless the relative humidity is very high (with an optimum of 100%) they are unable to spin adequate cocoons and so shrivel up and die (Thielmann 1938). Many of the above mentioned larval habits can be explained on these grounds; humidity, for example, will vary greatly between the upper and underside of a leaf, in or outside a mine, or gall or cocoon. Heavy rain can be very destructive by washing larvae off their foodplants. As to lethal temperatures, prepupae with their suspended animation are very resistant (Balch, 1939, found that some prepupae of *Gilpinia hercyniae* Htg. (Diprionidae) died at 0° F. and none survived —22° F., but some larvae actually survived 16° F.); but many feeding larvae, especially young larvae, are destroyed by early or late frosts. To bring resting prepupae out of diapause low temperatures are often necessary, but in some species such as *Acantholyda posticalis* Matsumura (=*pinivora* Enslin) (Pamphiliidae) two or three years' diapause for the prepupa is normal, one winter being quite exceptional (Scheidter 1926), while in *Gilpinia hercyniae* Htg. prepupae may rest for up to six winters before emerging (Prebble 1941).

In rearing sawflies very dramatic emergences of host or parasite may result from unnoticed strange larvae that have entered a gall or twig or tube-cork. All peat or cork or other substance provided for larvae to bore in should first be sterilized by baking.

The feeding period of larvae varies enormously according to

species, sex, foodplant, climate, season, etc. Wood-borers are generally much slower in growing than leaf-feeders; 2 to 3 years is the normal growing period in Siricidae (Chrystal 1928) and 1 year in Xiphydriidae (Chrystal and Skinner 1932). Species feeding on evergreens also appear to develop more slowly than those on leaves with high water content. On the whole 10 to 30 days is the normal time for British sawflies, but the scope of variation in single species is shown by Kemner's estimate (1924) of 19-27 days for *Nematus* (*Pteronidea*) *ribesii* Scop. Tenthr. (Nematinae) in Sweden compared to Wulker's (1926) 8-10 days in Germany, and Martelli's (1932) record of 13-14 days in the spring brood of *Athalia rosae* L. (Tenthr. Blennocampinae) in Italy compared to 28-30 days in the autumn brood. *Tenthredopsis* (Tenthredininae) varies from a few weeks in summer to five or so months in the autumn and winter, for larvae hatching in the late summer continue to feed at night right on till December (Benson 1936), or if not full grown by then perhaps right through the winter till the spring, for more than one lepidopterist has told me of finding the larvae at night in March. Estimates for the number of instars vary from 4 to 8; the males of a species often have one fewer than their females, feed for a correspondingly shorter period and grow to a correspondingly smaller size.

The number of annual broods is often uncertain but probably the majority of sawflies are single brooded in Britain. This may, however, be obscured by delayed emergence, so that a single brood is spread over the whole summer. At any rate *one* is typical for *Amauronematus* (Nematinae) and all such northern forms, for *Dolerus* (Selandriinae) and for most Tenthredininae; those that have more than one brood are potentially many-brooded under suitable climatic conditions, but the actual number, when more than one, is difficult to estimate through overlapping of the broods. Miles (1932) shows this clearly in his analysis of the annual cycles in the *Ribes* infesting sawflies in Britain. Starting with overwintering prepupae of *Nematus* (*Pteronidea*) *ribesii* Scop. and tracing them through one year he found the following different stocks: (1) Adults emerging in May and passing rapidly through three generations with flight-periods in May, end of June, and middle of August, passing into diapause in mid-September; (2) offspring of the May adults that went into diapause at the beginning of June and remained thus for the rest of the year; (3) offspring of May adults that delayed emergence till the end of July and produced offspring that went into diapause at the end of August; (4) offspring of the second flight (end of June) of stock (1) that went into diapause in mid-July; (5) stock with first flight delayed until the beginning of July with offspring that had a flight at beginning of September and produced larvae that went into diapause at the end of September; (6) offspring of first

flight of (5) which went into diapause in the middle of August. By the above it can be seen that although the maximum number of annual generations in any one stock is three, different flight periods occurred: (i) At the beginning of May; (ii) at the end of June; (iii) at the beginning of July; (iv) at the end of July; (v) in the middle of August; and (vi) at the beginning of September. In nature other combinations on the same theme probably occur, further confused by forward males of one stock copulating with straggling females of another stock. In *Pristiphora pallipes* Lepeletier, on the other hand, Miles found that his stock produced four rapid generations, no prepupae going into diapause until the end of September. While in *Nematus* (*Pteronidea*) *leucotrochus* Htg. only one annual generation was produced, all the offspring of the first flight going into diapause at the beginning of June.

The odd late summer emergences of *Dolerus*, etc., in this country are probably delayed individuals. The species with potentially more than a single annual brood are all either Argidae, Cimbicidae, Diprionidae, or Tenthredinidae mostly of the subfamilies Nematinae and Blennocampinae. Of all the other families, including the more primitive ones, no species is known that has more than a single generation a year, and many species take more than a year for a single generation. In species with more than one brood a prepupa normally only goes into diapause with the declining temperature at the end of the season, while in the single-brooded species the prepupa, whatever the prevailing temperature is, always goes into diapause; the cold winter temperature, as in many other insects, generally seems to be a necessary factor in bringing the prepupa out of diapause. Some species may have genetically fixed races that are always single-brooded (whose prepupae always go into diapause) and races that are potentially many-brooded (whose prepupae only go into diapause below a certain temperature) (see Prebble 1941).

The tendency for the northern races to be genetically fixed as single-brooded possibly finds its explanation in a greater general tendency to diapause; to enter into it and to remain in it. Balch (1939) found, for example, that in *Gilpinia hercyniae* Htg. the percentage of overwintering prepupae to produce adults in the following year increased from north to south. Theoretically it would appear that under favourable conditions a species having several broods a year has a very much greater potential increase than one with but a single brood; on the other hand, in uncertain climatic conditions, it would be a great advantage to have a percentage of individuals always in diapause so that abnormally bad weather conditions will not exterminate the whole colony of a species. Climate would thus be expected to select races with a greater

tendency to dippause in northern regions with uncertain climates and with a lesser tendency to diapause in those southern regions with more equable and favourable climates.

Very instructive have been Prebble's (1941) recent studies of diapause and related subjects in *Gilpinia hercyniae* (Diprionidae) in North America. He found among other things that an abnormally dry spring affects the one-generation and two-generation strains differently. In the one-generation strain he found that, after a dry spring, increase of rain after mid-June would be too late to affect the overwintering cocoons for that year; and the tendency would be to prolong the diapause by another year. In the two-generation strain individuals failing to develop in the spring through drought may respond to rainfall later in the season; and the result is a late and protracted emergent period.

In captivity prepupae often emerge from their earthen cells and come up to the surface of the soil during their diapause; they then may bury themselves again in some new position. This I have observed in a *Dolerus aericeps* Thoms. (Tenthredinidae, Selandriinae) which in mid-winter came up to the surface and then later buried itself again in a new position against the edge of the glass jar it was in. Likewise many of a colony of prepupae of *Neurotoma saltuum* L. (*Pamphiliidae*) came up to the surface of the soil and then went down again. This did not prevent the ultimate successful emergence of the adults. Peacock (1922) records the same for *Apethymus abdominalis* Lep. (Tenthredinidae, Blennocampinae). MacGillivray (1913) speaks of it as a common feature of resting prepupae. Ross (1937) records pupae of *Megaxyela langstoni* Ross (Xyelidae) coming up to the surface of the soil and the adult shedding the pupal skin here. Whether these habits are peculiar to sawflies in captivity is not known.

(*c*) Symbiosis between Fungi and Wood-borers

Several papers have been written lately on the symbiotic association between fungi and the wood-boring Siricidae and Xiphydriidae. The most complete study is that of Francke-Grosmann (1939) and the most recent by Parkin (1942), in which further references can be found.

Francke-Grosmann detected symbiotic fungi in four Siricidae on coniferae "*Sirex gigas*," "*Sirex juvencus*" and "*Sirex noctilio*," and one on angiosperm trees "*Tremex fuscicornis*." She was not able to detect any fungi in *Xeris spectrum* L. (coniferous trees). There seems to be some discrepancy as to how the fungi are transmitted during metamorphosis, but eggs apparently become infected at the start of their passage down the ovipositor. Fungal ovidia from the eggs readily give rise to hyphae in culture; young larvae have been fed for three weeks entirely on cultured hyphae, likewise have half-

grown larvae for as long as three months. It seems probable that the larvae in their tunnels feed on the hyphae ingested with the wood, or the fungi may simply make the wood palatable; the larval gut is certainly simpler than that generally found in larvae digesting wood. Furthermore, larval tunnels are always infested with the fungus, but the rest of the wood need not be. Francke-Grosmann thought that the individual species of Siricidae were not always associated with the same fungus although one fungus species does appear to predominate in each Siricid; Parkin says that in many samples from *Urocerus gigas* L. and *Sirex cyaneus* F. he and Cartwright only identified one fungus—*Stereum sanguinolentum* (A. and S.) Fr., while Clark, in dealing with *Sirex noctilio* F. introduced into New Zealand, found the same fungus there. In *Xiphydria prolongata* Geoffr. (*Salix*) Cartwright (1938) found a similarly symbiotic fungus resembling *Daldinia concentrica* (Bolt.) Ces. et de Not.

An important aspect of this is that these fungi are serious wood-destroying fungi that might be conveyed by the wood-wasps. The larvae can only develop in wood in a condition favourable for these fungi to develop; if, however, the humidity is too high the fungi develop too quickly and destroy the larvae. Hanson (1939) notes that Siricid larvae never burrow in conifers infested with *Fomes annosus* Fr., and often die when tunnelling through wood decayed by *Armillaria mellea* Vahl., although trees infected by these fungi are attractive to adult Siricidae for ovipositing.

(*d*) Humidity

As a high relative humidity seems to be one of the vital ecological factors for sawflies, owing probably to the very thin sclerotinous covering of most sawflies in all stages, it might be as well to collect together here a summary of what is said about humidity in the other chapters.

The adults must be sought in humid climates or humid seasons (such as during or just after rainy periods), or in humid localities (such as marshes, woods, mountain tops and so on) and in the early morning or evening on hot days. The optimum humidity for many eggs, larvae, prepupae and adults is nearly 100%. This finds its expression in various devices to set up microclimates of high humidity: eggs embedded in plant tissues; larvae feeding within plant tissues, on the undersides of leaves or in rolled leaves, or feeding only at night and hiding away in the day. In various species cocoons can only be made successfully in almost 100% humidity. Within the cocoon or cell the humidity must be maintained at almost 100% if the prepupae are to survive and the resulting pupae are to develop into adults. Even then if the cocoons are too dry they are too hard and the adults are unable to emerge. Many adults thus die

in their cocoons without managing to get out. Cocoons or cells are thus often made within plant tissues or beneath the soil; those that are not (certain Diprionidae, Argidae, Cimbicidae and summer broods of certain Nematine Tenthredinidae) are of parchment-like impervious material, often double, an inner cocoon within an outer one.

(*e*) Economic Importance of Sawflies

Several species of sawflies on the British list are more or less constant economic pests; a great many more have appeared as pests locally or spasmodically; others, so far innocuous or almost innocuous in this country, have appeared as pests on the continent of Europe or when accidentally introduced into North America. It is not proposed here to list all the species that have at one time or another been recorded as pests in this country; even if this were done there would still be many more potential pests. Many of them are aliens in our fauna, introduced with the crops or trees or flowers they infest; not true natives, as they feed on none of our wild plants (Benson 1935).

Probably the most dramatic pests in this country have been *Athalia rosae* L. (Tenthr. Blennocampinae) on turnips and *Pristiphora erichsoni* Htg. (Tenthr. Nematinae) on larch; both, in their time, a very serious threat to our country. The turnip sawfly came into prominence at about the beginning of the eighteenth century, probably as an immigrant, as it appeared first on the east coast. It was seen flying in from the sea and was washed up in swarms on the shore (Marshall 1783, Newport 1838 and Cameron); it thrived in hot dry summers and fell off in cool wet ones. It spread all over south England northwards and reached Ireland, but scarcely penetrated Scotland. At about the time of the accession of Queen Victoria it disappeared dramatically; some put this down to new crop rotations, but the real cause is unknown. By the end of the nineteenth century it was almost extinct and only occurred as a stray vagrant on the sea coast. In 1945, following several years of continued increase and spread on the continent, it began to appear again in south-east England, and from then onwards it has continued to spread over south England.

Pristiphora erichsoni Htg. caused its devastations in the larch plantations in the north of England at the beginning of the present century (Long 1913). It was a serious threat at the time, but now seems to have settled down as a normal member of our alien fauna.

Our most important more or less constant pests on fruit trees are: *Nematus* (*Pteronidea*) *ribesii* Scop. and *Pristiphora pallipes* Lep. (leaf-feeders on red-currant and gooseberry), *Hoplocampa testudinea* Klug (apple fruit-borer), *H. flava* L. (plum fruit-borer), *Caliroa*

limacina Retz. (pear and plum leaf slug), all belonging to the family Tenthredinidae.

Our coniferous trees are attacked by wood-boring Siricidae (*Urocerus gigas* L., *Sirex cyaneus* F., *juvencus* L. and *noctilio* F., both by the wood-boring activities of their larvae and by the ovipositing females conveying destructive fungi (see Section 3 (*c*)); by the needle-feeding Diprionidae (chiefly *Diprion pini* and *Neodiprion sertifer* Geoffroy on pine) and by Nematine Tenthredinidae (various species of *Pristiphora* and *Nematus* (*Pachynematus*)) which are locally common on larch and spruce: our corn and meadow-grass by the stem-boring Cephidae (chiefly *Cephus pygmaeus* L. and *tabidus* F.) and by numerous leaf-feeding Tenthredinidae.

Basket and cricket-bat willows are attacked by many Nematine Tenthredinidae, but generally without much damage, though the Nematine *Nematus* (*Euura*) *ater* L. and the Xiphydriid *Xiphydria prolongata* Geoffroy are accused of being vectors of *Bacterium salicis*, the cause of water-mark disease.

Further information about the occurrence of any species as a pest will be given in the systematic paper. Sitowski (1925) speaks of the value of Diprionidae in pine forests, unless they are in excessive abundance as, he says, they support numerous Tachinid and Ichneumon parasites useful in combatting other forest insect enemies. The argument, if sound, would appear to be much more widely applicable.

(*f*) Enemies of Sawflies

(i) **Insects**

In not many sawflies has the biology and biotic community of parasites, inquilines, predators and so on been studied in detail with adequate taxonomic study.

Some idea of the complexity of such communities can be gained from the paper by Carleton (1939) on English *Nematus* (*Pontania*) *proximus* Lep. s.l. and the paper by Salt (1931) on English *Cephus pygmaeus* L.

Carleton lists the following parasites, inquilines and predators as without doubt having been bred from the galls of *Nematus* (*Pontania*) of the *proximus* group:

Ichneumonidae:

Angitia vestigialis Ratz., *curvicauda* Holm., and *coleophorarum* Ratz.
Erromenus analis Br.
Ischnobatis stramineipes Br.
Limneria clypeata Br.
Meloboris crassicornis Grav.
Mesoleius bilineatus Grav., *crassicornis* Grav. and *variegatus* Jur.
Mesochorus sp.
Pimpla vesicaria Ratz.

Scopimenus pygobarbus Roman.
Tryphon leucodactylus Ratz.

Braconidae:

Microbracon discoideus Wesm. and *picticornis* Wesm.

Chalcididae:

Eulophus tischbeinii Ratz.
Eupelmus urozonus Dalm.
Eurytoma aciculata Ratz.
Habrocytus capreae Thoms.

INQUILINES: Coleoptera:

Balanobius salicivorus Payk.
(with its parasites: *Thersilochus flavicornis* Thoms. and two that also attack the *Nematus* (*Pontania*): *Pimpla vesicaria* and *Habrocytus capreae*).

Lepidoptera:

Tortrix podana Scop.
Peronea logiana Schiff.

In addition, various casual inhabitants of the galls include the Chrysomelid *Phyllodecta vulgatissima* L., Aphididae and so on, together with their associated parasites, and Acarina.

Salt (1931) made a detailed study of the parasites of *Cephus pygmaeus* L. in England with a view to introducing some of them into North America to combat the very closely related *C. cinctus* Norton. He lists the following primary and secondary parasites in the samples studied, together with the percentage infestations.

Primary parasites:

Hemiteles hemipterus Fabricius (Ichn., Cryptinae); 0.66.
Leptocryptus bellulus Kriechbaumer (Ichn., Cryptinae); 0.02.
Microcryptus (?) *unifasciatus* Schmiedeknecht (Ichn., Cryptinae); less than 0.0001.
Pezomachus fallax Förster (Ichn., Cryptinae); less than 0.001.
Pimpla detrita Holmgren (Ichn., Pimplinae); 2.12.
Collyria calcitrator Gravenhorst (Ichn., Pimplinae); 62-25.
Microbracon terebella Wesmael (Braconidae, Braconinae); 2.77.
Pleurotropis benefica Gahan (Chalcididae, Eulophinae); 3.95.

One species attacks *Hemiteles hemipterus* as a secondary parasite:
Hemiteles inimicus Gravenhorst (Ichn., Cryptinae).

Four species attack *Microbracon terebella* as a secondary parasite:
Hemiteles hemipterus Fabricius (Ichn., Cryptinae).
Pezomachus terebrator Ratzburg (Ichn., Cryptinae).
Eurytoma appendigaster Swederus (Chalcididae, Eurytominae).
Habrocytus sp. (Chalcididae, Pteromalinae).

Several insect orders will now be considered separately.

HYMENOPTERA

As at present known the greatest wealth of species parasitic on British sawfly larvae are found among the Ichneumonidae and in preparing this paragraph I am therefore much indebted to my colleague John F. Perkins, who has made a special study of them.

As far as this country is concerned certain tribes of this family, namely Cteniscini, Tryphonini (subtribes Tryphonina and Polyblastina), Mesoleptini (subtribes Mesoleptina, Mesoleiina, Perilissina, Euryproctina, Notopygina, Catoglyptina) and Collyriini—all of which are included in the composite subfamily Tryphoninae—, Rhyssini (Ephialtinae) and Adelognathini (Cryptinae) are almost exclusively confined to sawfly hosts. Certain other tribes contain genera which are, for the most part or wholly, parasitic on sawflies: of these may be mentioned *Aptesis* (Cryptinae, Aptesini) and *Stylocryptus* (Cryptinae, Phygadeuonini), Delomerista (Pimplinae, Ephialtini), and *Holocremnus* (Ophioninae, Campoplegini), but many species occur scattered in genera which are predominantly parasitic on hosts belonging to other groups of Hymenoptera, or to other orders of insects. The only large subfamily, from which no species have been recorded as parasitising sawflies, is the Ichneumoninae.

The largest and most conspicuous Ichneumonidae on sawflies are *Rhyssa persuasoria* L. on Siricidae, *Rhysella curvipes* Grav. on Xiphydriidae and *Opheltis glaucopterus* L. on Cimbicidae, but there are many other very striking insects among them. Some of the most remarkable are the Cteniscini and Tryphonini in which the stalked eggs of the fully mature females are extremely large and are carried on the ovipositor by the stalks. Most genera of these tribes carry a single egg, which frequently lies concealed beneath the large hypopygium; but *Polyblastus* (s.s.) and *Labroctonus* (=*Nemioblastus*) carry a cluster of eggs which are quite exposed, as the hypopygium is retracted, which gives the females of these genera a unique appearance. The eggs, when laid, are attached by the stalk to the integument of the host; the larvae are ectoparasites. A summary of the biology of these tribes can be found in Clausen (1941).

Comparatively little is known about the exact hosts of most species of Ichneumonidae parasitising sawflies for little rearing of numbers of larvae has been undertaken except in those species studied for economic reasons. This is natural as few entomologists have the time or opportunity to undertake large-scale breeding of collected immature stages of insects, and, what is more, collecting this material from as many different localities as possible. When it is seen how few records there are of the breeding of some of the commonest species of sawflies, it is not surprising that parasites of them have never yet been reared or preserved. Furthermore,

there are great difficulties in rearing many species of their sawfly hosts; and to be certain that the parasites bred came from the particular host requires still greater skill of management not always appreciated. A good example of this is the genus *Dolerus* (Tenthr. Selandriinae), of which many of the species require specialized conditions for rearing and these conditions favour the introduction of other hosts into the breeding cage.

Thus it is not surprising that little is known of the parasitism of sawflies by the other families of parasitic Hymenoptera, for there are comparatively few species in these families that are on sawfly hosts. In the Braconidae various isolated species (e.g. of *Microbracon*) have been recorded from sawflies, while *Ichneutes* and *Proterops* (Ichneutini) are parasites of Nematine Tenthredinidae and Argidae respectively.

Aulacidae have been bred from Xiphydriidae, e.g. *Aulacus striatus* Jur. from *Xiphydria camelus* L. in Holland (Smits van Burgst 1920), and Trigonalidae are chiefly parasites or hyperparasites through Tachinidae or Ichneumonidae on sawfly or lepidopterous larvae. Again in the Chalcidoidea the records refer to scattered species; species of *Tetrastichus* and related genera frequently attack sawfly eggs; *Trichogramma evanescens* Westwood was reported by Boas (1933) as responsible for controlling an outbreak of *Cephalcia arvensis* Panz. (Pamphiliidae) in Denmark; Ho (1936) records 80% of the larvae of *Syrista similis* Mocsáry (Cephidae) as attacked by Chalcids in Japan. Thalenhorst (1942) diagnoses the collapse of a serious outbreak of *Diprion pini* L. (Diprionidae) in Germany in 1939-40 as largely due to the egg parasites *Anchrysocharella ruforum* Krausse and *Tetracampe diprioni* Ferrière.

The Cynipoidea contain as sawfly enemies only *Ibalia leucaspoides* Hochenw. (Ibaliidae), the well-known parasite of Siricidae.

Proctotrupoidea have also been recorded from sawfly eggs; Shiperowitsch (1927) speaks of them as one of the controlling factors of Diprionid eggs in the Ukraine and Scheidter (1919) says that eggs of *Diprion pini* L. are sometimes heavily infested by a species of *Teleas*.

In the Hymenoptera Aculeata the Cleptidae have sawfly hosts, *Cleptes nitidula* F. attacking, for example, the currant sawfly, *Nematus* (*Pteronidea*) *ribesii* Scop. There are several records of *Vespula* taking sawfly larvae as prey. Cuthbert (1914) says that when clearing gooseberry bushes of the larvae of *Nematus* (*Pteronidea*) *ribesii* Scop. he found queen-wasps preying on them. *Vespula austriaca* Panz., *norwegica* F. and *germanica* F. were the species noted; the queens were later supported by workers of *V. norwegica* F. Watson (1922) also mentions queen and worker *Vespula* attacking *N. ribesii*. André (1881, p. 477) quotes De Siebold

to the effect that sawflies and their larvae are chewed up by wasps into a kind of food mash. Nevertheless, Bischoff (1927, p. 147) quotes from Roubaud to the effect that sawfly larvae are immune from the stings of wasps and humble-bees!

Friend (1933) records *Polistes pallipes* Lep. removing larvae of the birch-leaf miner *Fenusa pumila* Kl. (Tenthr. Blennocampinae) from its mines in North America. He also records ants attacking these larvae after they had left their mines and were entering the soil. Severin (1920) records *Formica rufa* L. and *Lasius niger* L. attacking larvae of the web-making *Neurotoma inconspicua* (Pamphiliidae) in North America, but only when these were full-fed and had come out of their protective webs to enter the ground or for some other reason were not sufficiently protected on the trees by a good covering of web.

I might here add that when I was in Switzerland in June, 1935, I found that where the lower mountain slopes were infested with *Formica*, patches of dwarf *Salix* were poor in sawflies, but that as soon as one came to cleared areas where, being still surrounded by snow, they were unmolested by ants, Nematine sawflies abounded on the catkins of the dwarf *Salix*. On the lower slopes any large *Salix* patch was continuously being searched by ants, and sawflies, as I watched, could scarcely settle unmolested. Many ants were observed carrying off adult and larval Nematinae of the genera *Amauronematus*, *Pristiphora* and so on. So much was this so that I wondered at the time how any sawflies attached to these herbaceous *Salix* could ever escape these marauding ants. Likewise my friend Dr. René Malaise tells me that in Burma he found that the upper limit of ant predominance marked the beginning of sawfly increase. We may thus expect a rich sawfly fauna to be found on the high mountains of the tropics and sub-tropics.

Finally some of the carnivorous sawfly adults prey on the adults of smaller species or even the smaller males of the same species (see 3 (*h*) Adult Feeding and Copulation).

DIPTERA

Certain Tachinidae commonly parasitise sawfly larvae; a complete list of known records of British sawflies thus attacked is given by Audcent, 1942. Hobby (1931) records three British Asilidae as having been found with adult sawflies as prey: *Dioctria oelandica* L. with *Tenthredo ferruginea* Schrank, *Tenthredopsis litterata* Geoffroy and *T. coquebertii* Klug; *Dioctria rufipes* Degeer with *Ametastegia glabrata* Fallén, *Eutomostethus luteiventris* Kl. ("*Blennocampa assimilis* Fallén") and *Dineura stilata* Klug; *Pamponerus germanicus* L. with *Dolerus niger* L., *Nematinus abdominalis* F. ("*N. fuscipennis* Lep.") and *Tenthredo atra* L. Hobby (1932(3)) records the Asilid

Dioctria rufipes Degeer as being found with *Nematus* (*Euura*) *ater* L., *Selandria serva* F. and *Tenthredopsis nassata* L. as prey.

Hobby (1931(2)) records the Cordylurid *Scatophaga stercoraria* L. with *Ametastegia glabrata* Fall. ("*Taxonus glabratus* Fall.") as prey.

COLEOPTERA

The weevil *Belanobius salicivorus* Payk. is described by Carleton (1939) as laying its eggs in the galls of the *proximus* group of *Nematus* (*Pontania*) (Nematinae) in England; the weevil larva devours the gall and destroys the sawfly host. In some seasons the weevil is extremely common locally, destroying up to 40% of the galls. The ichneumon *Pimpla vesicaria* Ratz. and the chalcid *Habrocytus capreae* Thomson, normally parasites of the sawfly host, feed alternatively on the weevil larva; this exemplifies a well-known principle in host-selection, that the environment of the host is often more important than its taxonomic affinities. Another ichneumon *Thersilochus flavicornis* Thoms. also bred from *Nematus* (*Pontania*) galls, is, on the other hand, apparently extensively a parasite of the weevil.

Two other weevils *Apion minimum* Herbst and *Balanobius crux* F. are also recorded as attacking *Nematus* (*Pontania*) galls of the *proximus* group in a similar way in France, and *Anthonomus sycophanta* Walsh as attacking galls of *Nematus* (*Pontania*) *hyalinus* Norton in North America (Marlatt 1896). Severin (1920) records the Coccinelid *Adalia bipunctata* L. as attacking larvae of *Neurotoma inconspicua* Norton (Pamphiliidae) in North America. Kapuscinski (1934) records the Dermestids *Megatoma undata* L. and *Globicornis corticalis* Eich. as preying on hibernating prepupae of *Pseudoclavellaria amerinae* L. (Cimbicidae) in Poland and Nägeli (1936) records that Coleoptera in Switzerland have been found to destroy up to 90% of some samples of the prepupae of *Pristiphora abietina* Christ. in their cocoons during the winter. Enslin says that Carabidae and Staphilinidae eat sawfly larvae.

LEPIDOPTERA

Carleton (1939) records two Lepidoptera as incidentally sometimes devouring galls of *Nematus* (*Pontania*) (Tenthr. Nematinae) together with the sawfly hosts: *Tortrix podana* Scop. and *Peronea logiana* Schiff. Marlatt (1896) records a lepidopterous larva in North America likewise devouring *Nematus* (*Pontania*) galls.

THYSANOPTERA

Marlatt (1896) also records Thysanoptera as attacking eggs and larvae of *Nematus* (*Pontania*) in North America, while Knechtel (1931) records *Thrips tabaci* Lind. as sucking eggs of *Rhadinoceraea reitteri* Knw., in Roumania.

HEMIPTERA

Nymphs of Pentatomidae frequently prey on sawfly eggs and larvae. *Picromerus bidens* L. is recorded as preying on larvae of *Pristiphora laricis* Htg. (Tenthr. Nematinae) in Germany (Hsin 1935) and on the larvae of *Neodiprion sertifer* Geoffroy (Diprionidae) in Saxony (Gäbler 1937). Sitowski (1925) mentions three species, *Eurydema oleraceum*, L., *E. festivum var. decoratum* H.S. and *Chlorochroa juniperina* L., as destroying many Diprionid eggs in Poland. Chapman (1922) records the Cimicid *Anthocoris nemorum* L. ("sylvestris") and *confusus* Reut. as destroying eggs of *Nematus* (*Pontania*) *piliserra* Thoms. in Surrey, and I have myself observed *Anthocoris* spp. attacking galls of *Nematus* (*Pontania*) *proximus* Lep. in Hertfordshire.

OTHER ORDERS

Enslin mentions Odonata as eating sawfly adults and larvae.

Severin (1920) records Odonata and Neuroptera (*Chrysopa*) as attacking adults and larvae respectively of *Neurotoma inconspicua* Nort. (Pamphiliidae) in North America. *Chrysopa perla* L. is recorded from France as attacking larvae of *Arge ochropus* Gmel. (Argidae) (see Feytaud 1913). Of Megaloptera, *Raphidia ophiopsis* L. is recorded as attacking eggs and larvae of *Cephalcia abietis* L. (Pamphiliidae) in forests of Upper Franconia (Lang 1897). Hobby and Killington (1934, pp. 43 and 45) record the Mecoptera *Panorpa germanica* L. ♂ as having been found with the remains of a *Nematus* (*Pontania*) sp. adult as prey, and *P. communis* L. ♀ with the fragments of a sawfly adult.

Finally in 1939 I had a whole brood of about 40 healthy half-grown larvae of *Nematinus caledonicus* Cam. (Tenthredinidae, Nematinae) in a sleeve on birch in my garden at Boxmoor destroyed by the earwig *Forficula auricularia* L. (Dermaptera).

(ii) **Spiders**

Bristowe (1941) points out that more invertebrates are destroyed by spiders than by any other animal order and concludes that whereas warning or protective colouration and resemblances are of no avail against spiders, on the other hand defensive movements, immobility, protective bristles or ejection from glands of stink or protective liquids are likely to be of effect against spiders which have highly developed olfactory and chemotactic senses. He makes the general statement (p. 312) that: "Sawflies generally seem to be distasteful to spiders. They are often rejected without being bitten, which is due to the spider's chemotactic sense. The larvae are also distasteful."

He quotes experiments in which adults of *Athalia liberta* Kl., *A. cordata* Lep. and *Tenthredopsis nassata* L. and a larva of *Dolerus* sp. were touched or even bitten by various spiders and then rejected, but gives one record of *Aglaostigma aucupariae* Kl. ("*Laurentia aucupariae* Kl.") in the possession of a spider. These records all refer to the single family Tenthredinidae and only to the subfamilies Athaliinae, Tenthredininae and Dolerinae. It suggests that sawflies are fairly successfully protected against spiders and that the Nematine Tenthredinid larvae with their stink glands, Tenthredinine larvae by their habit of ejecting liquid from the mouth, Cimbicid larvae by their ejection of blood from lateral pores, many larvae by their habit of dropping and feigning death, as well as the various inhabitants of galls, mines, fruit, stems, wood and so on, possibly largely escape the menaces of hunting spiders. Krausse (1919), however, reported that numerous adults of the Pamphiliid *Cephalcia abietis* L. were captured by the web of the spider *Linyphia phrygiana* during an outbreak in the Egge Mountains, Westphalia, but it is not clear that they were eaten. The fact that they were reported indicates that at any rate they were not set free to fly away.

The percentage table of sawflies blundering into spiders' webs and left to die there is not, of course, affected by whether they are eaten or later thrown out.

(iii) **Mammals**

Enslin speaks of squirrels, mice, moles and pigs as devouring numerous sawfly larvae, and various writers dealing with outbreaks of pests have drawn attention to the importance of vertebrate enemies of sawflies. Thus Hertz (1933), writing of the outbreak of *Diprion pini* L. (Diprionidae) in Finland in 1930-1, estimated that 71% of the overwintering cocoons were destroyed by small mammals, 10% by tits and other birds and only 13% by insect parasites. In the American spruce sawfly *Gilpinia hercyniae* Htg. (Diprionidae), Balch (1937) says that small mammals are the only important natural enemies. Likewise Graham (1929) writing of the outbreaks of *Pristiphora erichsoni* Htg. (Tenthredinidae, Nematinae) in North America says that mice and shrews, but especially mice, are the most important controlling agent, destroying 50-80% of the cocoons, while insect parasites and fungi together destroy only 10%. Unfortunately all such estimates were made only during serious outbreaks due presumably to a temporary eclipse of natural parasites in the first instance and to an absence of them in the second and third instances. The fact that insect parasitism was exceptionally low during the early stages of the outbreaks supports the view that insect parasites are the more important controlling agents.

(iv) **Birds**

Birds also devour sawfly larvae; as mentioned above, in an outbreak of *Diprion pini* L. in Finland, they were found to take a 10% toll of hibernating prepupae. According to Schedl (1939) tits and other birds tend to select the larger (♀) cocoons in preference to the smaller (♂) cocoons, while small mammals make no such selection. Sinz (1920) records tits, woodpeckers and starlings as destroying larvae of *Pristiphora abietina* Christ. (Tenthr. Nematinae) during an outbreak in Saxony in 1919-20.

Many other writers have recorded birds taking their toll during an outbreak. The larvae taken may even be brightly-coloured "aposematic" forms with well-developed stink glands as in the following two instances. Coward (1920) records that the larvae of *Nematus* (*Pteronidea*) *ribesii* Scop. (Tenthr. Nematinae), the common gooseberry sawfly, "are much sought for" by cuckoos and that "as many as eight cuckoos have been seen in one small group of bushes when the sawfly larvae have been defoliating the plants. The stomachs of two birds killed during the plague of these grubs were distended with the larvae."

Furthermore in the summer of 1925, when I had under observation a colony of larvae of *Croesus septentrionalis* L. (Tenthr. Nematinae) on a birch tree in my garden, they were discovered by a party of young chaffinches which would not leave them alone unless I stood under the tree; as soon as I moved away they devoured the lot.

Scheidter (1923) says that woodpeckers are the chief natural enemies of Siricid larvae boring in coniferous trees. Hanson (1939) however, found no evidence of this in the hundreds of *Sirex* infested logs he cut up and studied. Where the logs were attacked it was always in search of beetle larvae or, when old *Sirex* burrows had been attacked, it was in search of woodlice, hibernating flies, chalcids and so on.

Likewise *Sirex* adults were never attacked, though the larvae were extracted from the cut ends of logs by robins, wrens and tits. Enslin mentions woodpeckers, jays, cuckoos, nightjars, tits, thrushes, swallows, hedge-sparrows, hens, geese and pheasants as devouring sawflies.

Jourdain (1938-41) mentions records of sawfly larvae having been taken by the following species: the Northern Willow Tit, Eversman's Warbler, British Song Thrush, Redstart, Alpine Swift, British Great Spotted Woodpecker, Yellow Billed Cuckoo, Cuckoo, Bartram's Sandpiper, Lapwing, Black-headed Gull, Capercaillie, Scottish Ptarmigan and Common Partridge. This ignores many of his records where the description of the nature of the food might

be taken to be meant to include sawflies though they are not specifically mentioned.

In general it would appear that birds mainly attack sawflies when they are excessively abundant and that aposematic larvae with stink glands, hairs, etc., are not then any defence against birds. (See discussion under "Spiders" and "Mammals.")

(v) **Fish**

How often fish eat sawflies is not known, but it is interesting that Alfred Ronald in his Fly Fisher's Entomology (Mosely 1930) should have selected a specimen of *Dolerus niger* L. (Tenthredinidae, Selandriinae) as the type for his "Great Dark Drone."

(vi) **Reptiles and Amphibia**

Enslin records lizards and newts as enemies of sawflies.

(vii) **Nematode worms**

I have on more than one occasion found larvae of *Selandria serva* F. (Tenthredinidae, Selandriinae) in Hertfordshire parasitised by mermithid worms, but have never yet succeeded in rearing the worms, which cannot be named until mature. Riggert (1939) records *Mermis albicans* in larvae of *Athalia rosae* L. (Tenthredinidae, Blennocampinae).

(viii) **Fungi**

Prepupae overwintering in the ground are often destroyed by fungi. Thus Levtejev (1914) records that in Russia samples of *Pristiphora erichsoni* Htg. (Tenthredinidae, Nematinae) were infected sometimes to as much as 50-75%. Baird (1923) records the fungus *Isaria farinosa* Dicks as attacking the larvae of this species in Quebec and Long (1913) records a *Cordiceps* on it in Britain. Sinz (1920) records 8% of the larvae of *Pristiphora abietina* Christ. in Saxony destroyed by *Botrytis tenella* Sacc. Boas (1933) records larvae of *Cephalcia arvensis* Panz. (Pamphiliidae) in the ground attacked by *Botrytis tenella*, *Beauveria bassiana* (Bals) Vuill., *Spicaria* sp. and *Isaria farinosa*. Under 3 (*c*) "Symbiosis between Fungi and Wood-borers" I have already mentioned how Siricid larvae boring in wood may be overtaken and destroyed by a too luxurious growth of their own symbiotic fungi as well as by other fungi in the wood in which they are feeding.

(ix) **Bacteria and Viruses**

Sawfly larvae, especially in captivity, are often liable to bacterial and virus diseases. Shiperovitsch (1927) says that *Bacillus septicaemiae lophyri* is the main factor in controlling Diprionid outbursts in the Ukraine.

Downes (1925) records that many young larvae of *Priophorus viminalis* Fall. (Tenthredinidae, Nematinae) are killed by bacteria resembling *Coccobacillus acridiorum* in British Columbia.

Steinhaus (1949) gives details of bacterial and also of virus diseases in sawflies, notably polyhedrosis, which set back the infestation of *Gilpinia hercyniae* Htg. in Canada in 1939. In virus diseases the larva becomes filled with a dark brown fluid, as in many bacterial diseases, but this has an unpleasant odour and the skin ruptures; in bacterial diseases the skin remains elastic and the fluid contents are odourless.

(*g*) Protective Devices

(i) **In larvae**

Many of the devices that serve to protect the larvae from dessication also no doubt protect them somewhat against living enemies. Galls, mines, stem- and wood-borings keep the larvae out of the reach of spiders, ants and so on. Bristowe (1939, p. 105) lists a number of plants disliked by spiders; the list includes one or two specially favoured by sawflies and other insects, such as *Salix* foliage! Keeping to the undersides of leaves or to retreats in the ground during daylight perhaps places them out of the sight of many birds, but has not prevented them developing, in addition, the two extremes of colouring, inconspicuous (with solitary habit) and conspicuous (with social habit)—perhaps here developed against small mammals. These same extremes are developed with various other devices with the larvae that feed exposed and visible from above as well as with those that hide away. It is interesting that these two extremes are often both developed within a small taxonomic group of species. Thus you get closely related conspicuous (social) and inconspicuous (solitary) species, e.g. *Diprion pini* L. and *simile* Htg., and *Priophorus viminalis* Fall. and *ulmi* L.

These other devices can be classified roughly into visual, motortactic and chemotactic; though some may have a dual basis.

The visual class include:

Leaf-edge feeding

This is characteristic of many Nematinae on broad-leaf trees. The larva clings to the leaf-edge and when coloured uniformly green is very inconspicuous. This is enhanced by swinging the body to the underside of the leaf-edge when danger threatens from above, and vice versa. In narrow-leaved trees (conifers), grasses and so on the larva has no choice about being an edge-feeder; the body colour here is often broken up by longitudinal pale lines which render the larva very inconspicuous. In the low feeders this is combined with falling and feigning death when danger threatens.

Feigning death

This is characteristic of nearly all the inconspicuous larvae. They stop feeding and keep perfectly still when danger threatens. If danger comes too close and the plant vibrates or the larva is touched the spell ends and the responses are various: leaf-edge feeders cling tightly or drop, those on low-feeding plants drop, those with aggressive responses act accordingly.

Flattening against the leaf

This is also developed, chiefly in Nematinae, in those free-feeders that have not developed the leaf-edge-feeding habit, and anyway nearly always precedes that habit in the early stage larvae, which are probably thus better protected. In *Nematinus* and *Dineura* the larvae are flattened against the leaf and feed thus throughout, the former on the underside of the leaf, the latter on the upperside and eating only the upper layers of the leaf. It is also developed in all the Cladiini which are hairy larvae. In its extreme form we have the grotesque green woodlouse-shape of *Platycampus luridiventris* Fall. (Nematinae) which clings flat to the underside of the alder leaf. In *Caliroa* (Blennocampinae) the larva is masked with a slime covering (see below).

White bloom

A dusting with white bloom is characteristic of Cimbicid larvae and with most of the Blennocampinae that have not developed spines. It is mostly associated with under-leaf feeding, perhaps correlated with the paler leaf-green on the undersides of the leaves. In *Eriocampa ovata* L. it is developed into a thick white flaky substance, making the larva on an alder leaf look to all the world like bird-excreta.

The motortactic class include:

Covering with slime

This is best developed in the species of *Caliroa*; the common pear and plum slug, *C. limacina* Retz., being a black shining slimy larva feeding in company on the upper surface layers of a leaf surrounded by slime. They are conspicuous and may be distasteful to birds; but the slime probably keeps away ants and spiders.

Palisade

The larva of *Stauronema compressicornis* F. (Nematinae) is a leaf-edge feeder in company; it is green and inconspicuous in itself, but builds up a palisade of dried saliva round where it is feeding. The effects of this palisade are unknown; but it gives the appearance of fungus disease and additionally probably wards off marauding ants and spiders by tactile warning. The larvae being Nematinae also have stink glands which would certainly be distasteful to spiders and would enhance the warning.

Covering with hairs

There is much variation in the development of hairs even between closely related species. Hairs are very poorly developed in internal feeders (wood-borers, leaf-miners and so on) and are inconspicuous often in leaf-edge feeders, as might be expected, and in the last instar (prepupae) of all forms, but are well developed in certain under-leaf inconspicuous larvae (*Cladius*) as well as in some social conspicuous larvae (*Priophorus viminalis* Fall. and *Nematus* (*Pteronidea*) *ribesii* Scop. (Nematinae). In itself this seems to be no defence against birds, but may have some passive tactile effect on spiders; on touching it seems to activate the falling impulse and may be correlated with that.

Covering with conical or forked spines

Spines occur in many larvae. The large forked spines, peculiar to certain Blennocampinae are an alternative to the glabrous bloom-covering of other Blennocampine genera. Most of the fork-spined larvae are attached to pubescent Rosaceae. This class is possibly only a special development of the preceding.

Falling

This is a common habit when danger comes so near that the plant vibrates or the larva is touched, though some leaf-edge feeders on trees or larvae flattened against leaves usually cling all the tighter. In those species that eject from the mouth or lateral pores the actions are often combined. Falling might be considered as mainly visual in effect as the result is that the larva is lost in the under-growth, but since it is most highly developed in under-leaf low-plant feeders already hidden from normal vision its effect may be partly tactile, one of sudden motion when discovered by ant or spider.

Web spinning

This is characteristic of Pamphiliid larvae. It is used in the solitary larvae to hold together a leaf-roll and in social larvae to form a communal nest, spread over the foodplant, as in our *Neurotoma saltuum* L. In this species the bright yellow larval colour suggests a warning to birds. I have, however, mentioned above under "Enemies of Sawflies," 3 (*f*), how ants will only attack the larvae of a related North American species when these have come out of the nest or are insufficiently covered by it. The inference is that the web does act as a protection against ants.

The chemotactic class include:

Ejections from the mouth

Tenthredinine and Dolerine larvae when handled eject a liquid from glands opening in the neighbourhood of the mouth. This is combined with falling. Diprionid larvae raise the head and eject a liquid from the same region.

Ejecting blood from lateral abdominal pores

Cimbicid larvae eject blood from lateral pores one above each spiracle of abdominal segments 2-8. This is also combined with falling when the larva is touched. The blood and the liquid from the mouth, mentioned above, may have some caustic or other distasteful qualities.

Ejecting scent from ventral abdominal glands

Like the last two this feature is characteristic of a large taxonomic group, in this case the Nematinae. The gland openings are in the middle of the venter, one behind each pair of legs on the first to seventh segments. The glands are protrusible sacks; and the abdomen is turned up so as to expose the under surface when the glands are protruded at threatened danger. This waving of the abdomen may serve to warn the would-be foe, visually if it hunts by sight, tactilely if by touch. The ejection smells like benzaldehyde. In some social Nematinae it is so lavishly dispersed that I have even been able to track down a colony of *Croesus septentrionalis* L. after dark on a still night, discovering it by the scent as I walked nearby. In those Nematinae that have become adapted to a leaf-mining habit (*Pseudodineura*) or fruit-boring habit (*Hoplocampa*) or live entirely in galls (*Nematus* (*Pontania*) and (*Euura*)) the glands with their scent are still present and can be detected on opening the plant structures.

As suggested, under the earlier discussion on Enemies of Sawflies, 3 (*f*), this scent has probably been developed against spiders, as birds and mammals and ants readily eat Nematinae, while spiders are known to have highly developed chemotactic senses and have not been observed to eat Nematine larvae.

(ii) **In adults**

Aggressive colouring

Many of the wasp-coloured sawflies (*Tenthredo scrophulariae* L., etc., and the Siricid *Urocerus gigas* L., etc.) certainly deceive people into thinking they are wasps and hornets. There may be some significance in the fact that these good wasp-likenesses belong to groups which attack and devour other insects.

Other highly coloured sawflies can be classified into groups (independent of taxonomic relationships) which may belong to

Batesian or Müllerian mimicry associations. One of these has a bright yellow or orange abdomen with a black mesonotum (many Selandriinae, many Nematinae, all *Athalia*, and other Blennocampinae, as well as certain Argidae, etc.); another is mainly black with a blood-red mesonotum (including our Nematine *Hemichroa alni* L., our Blennocampine *Eriocampa ovata* L. and *Eutomostethus ephippium* Panz. and many exotic Selandriinae, Argidae, etc.).

Inconspicuous colouring

The largest group here is probably those with a green ground body colour (including many of our Nematinae and several Tenthredininae). It is mostly characteristic of females and serves to hide them when engaged in ovipositing; in males it is usually replaced by yellow. This is a common sexual physiological colour difference in the blood of phytophagous insects (see Wigglesworth, 1939, p.232), females having green blood, males pale yellow; the cause, whether a difference in chemical metabolism or of pigment absorption, is unknown. In some species such as *Amauronematus puniceus* Christ. (Tenthr., Nematinae) the female is green when she first emerges, but soon turns yellow.

Powerful mandibles

In the Cimbicidae and certain Tenthredinidae such as Tenthredininae, Dolerini of Selandriinae and Emphytini of Blennocampinae, powerful jaws have been developed and these are used in defence against enemies, as anyone knows who has handled these insects.

Feigning death

Many small Tenthredinidae, especially Blennocampinae and Nematinae, as well as Argidae (i.e. especially those sawflies with feeble mandibles), have a habit of dropping to the ground and feigning death when danger threatens. In this feint the wings and legs are folded up and the antennae are curved down beneath the body in the pose adopted by a pupa. The feint often lasts only until you touch the insect, and then it tries to run and fly away. When they fall into tangled undergrowth or matted turf and lie still, and so long as they lie still, they are extremely difficult to find; generally, however, the feint is not continued for long, and all you have to do is to wait perfectly still until the sawfly makes a movement and reveals itself.

(*h*) Adult Feeding and Copulation

Habits of adult sawflies have been referred to in many other sections, especially those under the headings "Field and Collecting Notes" 2, "Larvae and General Biology" 3 (*b*), "Humidity" 3 (*d*), "Protective Devices" 3 (*g*), "Dispersal" 4 (*a*), and "Parthenogenesis" 5 (*c*).

After extracting itself from the pupal skin, the adult remains some days within its shelter before emerging so as to develop and harden its sclerotinous covering. Eliescu (1932) estimated a delay of 1-7 days in *Diprion pini* L.; all other estimates fall within these extremes except in overwintering adults of Siricidae. On emerging, adults will feed and, shortly after this, females begin to oviposit, often without waiting for a male to find them. Males often emerge before females.

(i) **Feeding of adults**

Moisture (rain, dew, cuckoo-spit, honey-dew, ripe fruit)

Adults, especially when first emerging, readily imbibe moisture. I have observed *Tenthredo* ? *amoena* Gravenhorst at cuckoo-spit (from *Philaenus leucophthalmus* L.) eating the froth as well as the grubs, and even Nematinae, that are not normally attracted to flowers, at honey-dew and damaged ripe fruit.

Flowers and leaves

Nectar and pollen together with whole stamens and even petals are frequently taken, mostly by females. Umbelliferae with their easily accessible nectaries are generally considered to be the most popular, but this is partly due to the fact that they exhibit a large white or yellow umbel on which insects are easily seen; likewise Rosaceae with large inflorescences such as *Crataegus*, *Pyrus* and *Spiraea* are favoured, as well as yellow Compositae and *Ranunculus*: all of these flowers have a prolific pollen production. There is also a marked tendency for species to visit the flowers of their foodplant: *Tenthredo scrophulariae* L. feeds mainly at the flowers of *Scrophularia*; *Zaraea fasciata* L. favours flowers of *Symphoricarpos racemosus* L.; *Abia sericea* L. flowers of *Scabiosa*; *Arge gracilicornis* Klug *Rubus* flowers. *Macrophya punctum-album* L. actually eats the leaves of *Fraxinus*, its larval foodplant (Chawner 1921); while *Sciapteryx consobrina* Klug adults eat the edges of the leaves of their hostplant *Adoxa moschatellina* L. with apparent relish, "reducing them with a movement and rapidity like a rapacious larva" (Woollatt 1946). Early Nematinae attached to *Salix* feed at *Salix* catkins and are rarely found at other flowers; Xyelidae are voracious pollen-feeders, and the larvae feed also on pollen (*Xyela*) or on the leaves of catkin-bearing trees producing much pollen. This tendency may have some correlation with the choice of larval foodplant and will be further discussed (see Section 5 (*d*)). Apart from this characteristic the following are the main flower-haunting groups: Tenthredinidae subfamilies Tenthredininae, Selandriinae, Blennocampinae, Argidae, Cimbicidae and Cephidae. Of these the Tenthredininae are voracious feeders on other insects which they

catch at these flowers; and the males come there also to find the females. Tenthredininae, Dolerinae and in Switzerland the little Cimbicid *Coryna* frequently eat petals, especially of *Ranunculus*.

Pubescence on plants

Ross (1933 (1)) records that he has observed in North America *Sterictiphora apios* Ross (Argidae) and *Nematus* (*Pteronidea*) *mendicus* Walsh (Tenthr. Nematinae) cropping the pubescence of their hostplants "just as a cow crops grass" and suggests that this is probably a widespread habit though it has not been observed, so far as I am aware, by anyone else.

Other insects

Selandriinae (Dolerini), Tenthredininae (*Tenthredo*, *Macrophya*, *Tenthredopsis*, etc.) and Blennocampinae (Allantini) are very carnivorous and visit flowers partly to prey on small flower-haunting Diptera and Coleoptera; but they also attack other sawflies, even the males of their own species. Clausen (1940) records that according to Iwata, *Tenthredo nigropicta* Smith in Japan feeds extensively on larvae and pupae of Chrysomelidae of the genera *Melasoma* and *Plagiodera*, two or three full-grown larvae being eaten each day. *Dolerus niger* L. adults are mentioned by Korolkov (1914) as devouring Psyllid larvae in Russia. Males visit flowers mostly in search of the females and are less frequently observed feeding on other insects. Several British records of Tenthredinidae with named prey were given by Hobby (1932 (1) and (2)). Siricidae were likewise recorded by Bechstein and others as preying on other insects, but this was not confirmed by Chrystal (1938: 277). The habit is also recorded for Xiphydriidae; Matsumura (1927) says that adults of *Xiphydria kawakami* Mats. are a pest in Japan because they enter houses and carry away silkworms!

In the Cimbicidae we have Howard's note (1896) that "in the collection of the Gypsy Moth Commission" is "a specimen of *Cimbex americana* which it was definitely stated had been found flying with the larva of a gypsy moth in its grasp."

(ii) **Copulation**

The terminology for the different poses taken in copulation is Lamb's and is taken from Richard's discussion (1927).

Male vertical pose

In the primitive condition of the orthandrious sawflies the genitalia are not reversed (Cephidae, Pamphiliidae, Siricidae and Xiphydriidae). To generalize from Rohwer's observations (1915) on the North American *Xiphydria maculata* Say, the Xiphydriid male mounts the back of the stationary female, curving the tip of his

abdomen over to the underside of the tip of her abdomen. The parameres grasp "the side of the knob at the base of the sheath and the hypopygidium fits over the knob." Chrystal and Skinner (1932) describe the pairing in the British *Xiphydria prolongata* Geoffroy. They say that the males emerge before the females and spend some time tapping loudly with their abdomens on the logs in which the females are still resting. They also say that sometimes they observed a very small male copulate with a large female and that he clung to her upside-down, holding on to her sawsheath with all six of his legs. Snodgrass (1941) finds that Xyelidae contain strophandrious as well as orthandrious genera.

Linear pose

In the strophandrious sawflies (*Xyela* of Xyelidae, Argidae, Cimbicidae, Diprionidae and Tenthredinidae) the male has his genitalia upside-down, twisted at the base through 180°. This enables the sexes to approach each other backwards both remaining the right way up.

The female is usually settled and the male makes a dart at her, seizing her as he lands; with his hind legs he usually holds down her wings to prevent her flying away. Females often seem disinclined to copulate while the males, which are often outnumbered by females, are polygynous. The enlarged hind legs of many sawflies are usually exaggerated in males (*Tenthredo*, *Macrophya*, etc.), presumably for this purpose. In one experiment I snipped off the hind legs of a number of male *Tenthredo marginella* F. and enclosed them in a jar with a single female. The males made many attempts to copulate but, without their hind tarsi with which to hold down the wings of the female, the female always escaped.

In *Zaraea fasciata* L. (Cimbicidae) the male, according to Osborne (quoted by Cameron), departs from the normal linear pose by bending himself round and right under the female until his head reaches to about her middle legs. I have not been able to find out whether this habit is characteristic of all Cimbicidae; and in several other groups the copulation pose has never, so far as I am aware, been described.

As to the time taken in copulation in Tenthredinidae, most estimates vary between 1 and 2 minutes, but in *Tenthredo mesomelas* L. I have seen it completed in 30 seconds. Ries (1926), however, gives 10 minutes for *Cephus pygmaeus* L., while Enslin mentions a quarter to half an hour or more for *Cimbex* and records that females are sometimes found dragging a dead male attached to them. Chrystal and Skinner (1932) mention that the whole operation of pairing and copulation may last anything from 10 to 45 minutes in *Xiphydria prolongata* Geoffroy and that throughout the whole

operation the male may continue to brush the female antennae with his. Females often also paired with more than one male, laying eggs between the copulations.

Copulation usually takes place when the female is at rest on leaves in the sunshine, in flower-haunting species on the flowers of their choice when the females are engaged in feeding. Ries says that the *Cephus pygmaeus* L. he observed almost always copulated on yellow flowers, chiefly Cruciferae at the edges of cornfields. Siricidae are supposed to copulate high in the air or in the tops of trees. In many sawflies the females are often without any apparent desire to copulate, and have to be captured and held by the males. If they escape the males they merely proceed to oviposit parthenogenetically and thereby, in the normal course of events, produce entirely male offspring. Courting may take the form of communal sun-dances by the males. As males often emerge before females the aerial dances often seem independent of courting. For example, the males of *Dolerus niger* L. rise up from the pastures and cornfields, where their larvae feed, and hover in swarms over the surrounding trees, leaving and ignoring their females down in the fields. Cameron records the swarming of *Trichiosoma lucorum* L. males in hot sunshine over the tops of birch trees and says that they flew round in great circles making a loud *Bombus*-like buzzing. He says also that he once observed two males fighting for ten minutes by rushing at each other.

4. DISTRIBUTION

(*a*) Dispersal

(i) **Dispersal by air-currents or wing-power**

One of the most notable features of sawfly distribution is that they are apparently completely absent from such oceanic islands as the Hawaiian Islands, the Seychelles, Samoa and Galapagos. They are apparently scarce as natives in New Zealand (two endemic Xiphydriidae and one endemic Orussid), Madagascar (one endemic *Athalia* (Blennocampinae) related to African species, and two species of a peculiar endemic subfamily, Athetocephinae of Cephidae—a family otherwise confined to the northern hemisphere) and Madeira (only one species, *Pristiphora denudata* Konow (Nematinae), which is found also on the mainland of western Europe). From this it would appear either (1) that sawflies are not easily dispersed long distances in nature or (2) they are unable to survive or to reproduce after such dispersal.

The majority of sawflies, though poor fliers, are too large or too heavy compared to their surface area to be likely to be common inhabitants of the upper air; newly hatched larvae might of course

be carried up, but are scarcely likely to survive dispersal in this way. Adults are, of course, with other insects, readily blown up and landed on top of our highest mountains. When, for instance, I was climbing mountains in the Highlands of Scotland in 1931, 1932, 1934 and 1939 I several times observed the arrival of lowland sawflies on the mountains. I have already recorded (1935 (i)) the arrival of a specimen of the pine-feeding *Acantholyda posticalis* Matsumura (=*pinivora* Enslin) (Pamphiliidae) on the top of Ben Lawers in Perthshire (3,985 ft.) and of a female of *Dolerus haematodes* Schrank on the top of Benmore (Perthshire) (3,843 ft.)—a species I never found as a native at these heights. Likewise many of the sawflies collected near the top of Ben Nevis (4,406 ft.) by Capt. W. S. Bruce when he was stationed at the observatory there (Morice 1896), such as *Brachythops wüstnei* Konow (Selandriinae), only live normally in low country and had obviously been wafted up there.

The only definite records of a sawfly arriving across the sea and surviving the passage refer to the turnip-sawfly (*Athalia rosae* L. (Blennocampinae)) in England; Marshall (1783) records their arrival in clouds on the east coast, many afterwards being found washed up by the sea, heaped up in some places to a depth of two inches (for further references to the former immigrations and epidemics of this species in Britain see Tutt (1902) and Benson (1935 (2))). Scott (1926), however, records a swarm of insects washed up with the incoming tide at Bream, Somerset, in June, 1920. The swarm included Coleoptera, Tipulidae and sawflies—"a largish green and yellow ringed sawfly which was very numerous." "The fringe of dead insects was about half a mile long, and varied in width from one inch at the ends to three inches in the centre." The observations were made after a spell of hot calm weather. Champion added a footnote to say that two of the beetles (*Corymbites* spp.) are always found in hilly or mountainous country and must have come across from Wales. Benson (1946) recorded a vast swarm of *Athalia cordata* Lepeletier moving eastwards in north Devon in August, 1945.

As to the actual distance that a sawfly can travel in air-currents or on its own wing-power, we have little but inconclusive or negative evidence. Balch (1936) estimated that *Gilpinia hercyniae* Htg. (Diprionidae) in Canada can fly at least 1½ miles and probably much more, because adults taken alive from the middle of the St. John River were more than a mile from the nearest spruce plantation.

The scarcity of sawflies on oceanic islands or even islands near mainlands indicates that even if sawflies are readily transported they cannot survive or reproduce afterwards. No doubt their high humidity requirements would tell against their survival on long

journeys or on windswept islands, while the extreme specialization in foodplants of many species would render it less likely that, when transported a long distance, they could establish themselves, though any entirely female-producing parthenogenetic form would be highly favoured in that a single specimen might suffice to start a colony.

It seems likely that the peculiar cenchral wing-holding apparatus in sawflies, enabling them to hold their wings flat over the thorax when not in use, may enable them to escape being blown away in high winds. It would also then account for the prevalence of sawflies in arctic regions and on mountain tops, their absence from oceanic islands, and the rarity in the group of apterous and brachypterous forms.

(ii) **Dispersal by man**

On the other hand, sawflies are easily introduced by man; this applies chiefly to those species that feed or spend their resting stages in stems or wood, in straw or forest litter used for packing, especially if already attached to plants used by man and so cultivated near his settlements; some are also introduced in their resting cocoons among the roots of nursery stock. A glance at the quarantine records of pests intercepted on plants arriving in the United States shows this and so does the long list of pests introduced from one country to another. This list includes wood-borers (*Sirex noctilio* F. into Australia from Europe and various European and American Siricidae into Britain); corn-stem-borers (*Cephus pygmaeus* L. and *Trachelus tabidus* F. (Cephidae) from the European continent into Britain and North America); fruit-borers (*Hoplocampa testudinea* Klug (Nematinae) in apples from Europe to British Columbia and one or two *Hoplocampa* species from the European continent into Britain); forest leaf pests (*Gilpinia hercyniae* Htg. and other Diprionidae into North America from Europe, and various Nematinae and Diprionidae attached to conifers into Britain); leaf pests of fruit trees (*Caliroa limacina* Retz. (Blennocampinae) of European origin is now almost as cosmopolitan as the pears and plums it feeds on); leaf pests of other nursery stock (e.g. *Allantus cinctus* L. (Blennocampinae) and *Cladius difformis* Panz. (Nematinae), etc., on roses from Europe into North America).

In deciding what British species are entirely alien, in other words owing their existence in Britain entirely to inadvertent introduction by civilized man, I have included first all those sawflies attached only to plants owing their existence here entirely to man's introduction (e.g. *Picea*, *Larix*, *Robinia*, *Aruncus*, etc.). To these I have added, often with some doubt, those sawflies mainly attached to cultivated plants in gardens and plantations. For example, *Hoplocampa flava* L.

in Britain occurs mainly on cultivated plums, less commonly on *Prunus spinosa* L., etc., and is regarded here as an introduced species while the related native *H. chrysorrhoea* Kl. and *H. rutilicornis* Kl. in Britain are almost entirely on wild *Prunus* and but rarely on cultivated plums. The Diprionidae on *Pinus* listed below as aliens have not yet been found in the ancient Caledonian forests of Scotland; in these forests, on the other hand, occur the species; *Microdiprion pallipes* Fallén, *Gilpinia pallida* Kl. and *G. frutetorum* F. which have not yet been recorded from our southern plantations. Such species as *Xyela julii* Bréb. and *Sirex juvencus* L. occur both in the ancient forest and in new plantations in the south, and may be of native stock reinforced with introductions.

Many species attached to *Rosa* are of very wide palaearctic or even holarctic distribution. As *Rosa* has been cultivated and carried about by man from time immemorial, it is probable that some of the sawflies in Britain attached to *Rosa* are not native here (e.g. *Arge ochropus* Gmelin to judge from its Mediterranean concentration, and possibly certain species of *Allantus*, considering the ease with which they are introduced resting in stems). The very wide palaearctic or even holarctic distribution of most of the British sawflies attached to Polygonaceae (*Rumex* and *Polygonum, etc.*), and Chenopodiaceae is perhaps to be explained thus: (1) Several plants of these families are common weeds of cultivation; (2) others are widely cultivated and dispersed as herbs or forage crops; and (3) such sawfly genera as *Ametastegia* could in addition easily be dispersed in their resting stages which are spent in stem borings or soft wood. The basket willows, *Salix triandra* L., *viminalis* L., and *purpurea* L., have also perhaps been reinforced by cuttings introduced from abroad; in fact *S. purpurea* L. is only doubtfully native in Britain and probably not a native in Ireland. The sawflies peculiar to these plants may not, therefore, be native.

Man's indirect influence on insect distribution is likely to have been just as far-reaching as direct introductions. By clearing forest man has encouraged the spread and enormous increase of scrub, heath, grassland and open land types at the expense of the forest types, first of all probably along the ancient tracks and trade routes. But in so doing man has only continued, though greatly extended, what had already been started by such animals as beavers and the larger tertiary browsing vertebrates that preceded him. Furthermore, by cultivating and spreading plants, man has provided in advance for the natural spread as well as the inadvertent introduction of species associated with these plants. Some of these species seem to have spread or been brought by man from the open steppe country of the eastern Mediterranean (see discussion under "Types of Palaearctic Distribution," 4 (*d*)) and other early centres of

civilization; others probably formerly persisted precariously in accidental forest clearings, exposed hills, landslides, cliffs, sea coasts, margins of rivers and lakes in the same districts they occur in today, but their distribution has been favoured and spread beyond all recognition by man's destruction of the forest and turning of the soil. The correlation between the distribution of man with that of other animals and plants goes, however, far deeper; for man too was divided into races with distributions more or less in accordance with the distribution of the other floristic and faunistic types.

British species existing probably as introduced aliens

(Those included in square brackets [ ] are probably nowhere established in Britain.)

CONIFERAE

Pinus, *Picea* and *Larix*

? *Sirex cyaneus* F. (Europe or N. America.
? *S. noctilio* F. (Europe).
[*S. californicus* Norton (N. America).]
[*S. areolatus* Cresson (N. America).]
[*Urocerus augur* Klug (Europe).]
U. gigas gigas L. (Europe).
[*U. gigas flavicornis* F. (N. America).]
[*U. albicornis* F. (N. America).]
Xeris spectrum L. (Europe).

Pinus

Diprion simile Htg. (Europe).

Picea

Gilpinia hercyniae Htg. (Europe).
Nematus (*Pachynematus*) *scutellatus* Htg. (Europe).
N. montanus Zadd. (Europe).
Pristiphora saxeseni Htg. (Europe).
P. abietina Chr. (Europe).
P. compressa Htg. (Europe).
P. ambigua Fallén (Europe).
P. amphibola Htg. (Europe).
P. subarctica Forsslund (Scandinavia).

Larix

Anoplonyx duplex Lep. (Europe).
Nematus (*Pachynematus*) *imperfectus* Zadd. (Europe).
Pristiphora erichsoni Htg. (Europe).
P. wesmaeli Tischbein (Europe).
P. laricis Htg. (Europe).

FILICALES

Blasticotoma filiceti Kl. (Europe).

DICOTYLEDONES

Caprifoliaceae, *Lonicera*, *Symphoricarpus*, etc.: ? *Zaraea fasciata* L. (Europe).

Cruciferae: *Tenthredo flaveola* Gmel. (Europe).

Grossulariaceae, *Ribes*: *Nematus* (*Pteronidea*) *ribesii* Scop. and *leucotrochus* Hartig (Europe). *Pristiphora pallipes* Lep. (Europe).

Papilionaceae, *Robinia pseud-acacia* L.: *Nematus* (*Pteronidea*) *tibialis* Newman (N. America).

Ranunculaceae, *Aquilegia*: *Pristiphora alnivora* Hartig (Europe).

Rosaceae

Aruncus silvester (Kosl.): *Nematus* (*Pteronidea*) *spiraeae* Zadd. (Europe).

Geum: ?*Metallus gei* Brischke (Europe).

Prunus domestica L.: ? *Hoplocampa flava* L. (Europe).

Pyrus communis L.: *Hoplocampa brevis* K. (Europe). *Pristiphora abbreviata* Htg. (Europe).

Malus pumila Miller: ? *Hoplocampa testudinea* Klug (Europe). ?*Pristiphora maesta* Zadd. (Europe).

Rosa: ? *Arge ochropus* Gmel. (Europe).

Tiliaceae, *Tilia*: *Parna tenella* Kl. (Europe).

MONOCOTYLEDONES

Gramineae, *Avena*, *Hordeum*, *Triticum*, etc.: ? *Cephus pygmaeus* L. (Europe). ? *Trachelus tabidus* F. (Europe).

Liliaceae, *Polygonatum*: ? *Phymatocera aterrima* Klug (Europe).

(iii) **Sawflies as evidence of historical geography**

To summarize now what has been said in the two preceding sections, it is obvious that care must be exercised in making generalizations about the distribution of individual uniform species that may have been introduced by man. It is clear, however, that the only species likely thus to become established in a new country are those associated with native or introduced plants.

On the other hand, the vicarious distribution of subspecies, species groups, genera and higher categories, whose divergence preceded man's interference, would appear to offer very promising material for generalizations about historical geography, for all the evidence points to the great importance of certain geographical barriers in the natural dispersal of sawflies. In this characteristic they differ markedly from some of the groups of small parasitic Hymenoptera which have been very much more widely dispersed by natural means, being a common element of the upper air fauna.

I have already discussed the various probable factors involved and of these I attached special importance to the sawflies' special cenchral wing-locking device which enables them to avoid being blown away by winds.

(*b*) Distribution of British Species

(i) **Local lists**

It was originally intended to include in the Synopsis a detailed account of the distribution of British sawflies, species by species, extracted from the county lists and other published records. This plan was abandoned as many of the published records proved to be unreliable when the specimens on which they were based were examined. The published records, therefore, now need revising in the light of more critical taxonomy. For this reason, in the Synopsis I have limited my notes on the distribution of each species to general statements in the better-known species, and in the lesser-known or more critical species mainly to records of specimens seen by Dr. R. C. L. Perkins, F.R.S., or myself. The material on which the Synopsis is actually based, however, is mostly limited to that material that was readily available for re-examination as each new character was discovered, that is to say the material already belonging to the British Museum (Natural History) or on long-term loans.

The result is that the records are heavily weighted for South Devonshire (Perkins Collection), Hertfordshire and Buckinghamshire (Benson Collection), Surrey (Morice Collection), the Glasgow District (Cameron Collection), and the Scottish Highlands (Cameron and Benson Collections). The distribution records, therefore, are for the time being built round these focal points. The Irish records are partly from a list supplied by that indefatigable naturalist Mr. A. W. Stelfox, A.L.S., based mainly on specimens submitted to Dr. Perkins for confirmation, and partly from more recent specimens collected by Mr. R. C. Faris in Cavan.

These records are insufficient to give more than a very provisional idea of the distribution of sawflies in Britain.

That 77% (350: 456) of the known British sawflies should already have been found to occur in Hertfordshire and Buckinghamshire suggests that more species await discovery in Britain (Benson 1940 and 1943 (1) and unpublished data). From this it is obvious that almost the whole of Britain awaits more careful exploration: as areas likely to give surprises one might mention the rich south and south-east of England (Dorset, Hampshire, Sussex and Kent) and East Anglia; while it should be noted that north and central Wales, north-west Scotland and many parts of Ireland are almost entirely unexplored.

When we turn to the records of our British species outside Britain, to see how they are distributed there, we find: (1) that, except for large and conspicuous species, too few areas have been worked thoroughly enough for us to attach any significance to the supposed absence of a species there; (2) that in many cases we dare not accept records of occurrence, because we are not satisfied that sufficiently

critical taxonomy has been applied; and (3) that the further afield we go the greater has been the tendency for species to have been described as new without comparison with European material; we do not yet know, for example, how many more of the east Asian or North American species will ultimately be synonymised with European species or linked with them as geographical subspecies.

(ii) **Distribution of sawfly taxonomic groups**

If we compare all the sawflies recorded from Scotland and Ireland with those recorded south-east of a line taken from the Humber to the Bristol Channel, we find that most of the Scotch and Irish species occur also in the S.E. Those species peculiar to the north are mostly Nematinae; but many of our widely distributed species, Nematinae as well as others, have their headquarters in the Siberian Taiga. Most of the other groups, apart from the Nematinae, increase in the number of species represented as we approach the S.E. with its warmer summers and more continental climate. This is noticeably so in the Cephidae and large Tenthredininae such as *Macrophya* and *Tenthredo*. The Cephidae are unrepresented in Ireland and only one (*C. pallipes* Klug) occurs in Scotland, compared to 11 in the S.E.; *Macrophya* has but one species recorded from Ireland whereas 13 occur in the S.E.; *Tenthredo* has but 17 in Ireland compared to 31 in the S.E.

(*c*) Ecology and Biogeography

Distribution must be considered in relation to Ecology. The more or less close dependence of sawflies on special hostplants accordingly relates their distribution and ecology closely to that of these plants. The study of the ecology of sawflies can only proceed from the basis of plant ecology, which apart from the special sawfly relationship with individual plant species, is a rough "thermometer" of all the physical conditions of the environment. It is outside the scope of this paper to discuss plant-ecology as such and Tansley's textbook (1939) should be constantly consulted so far as Britain is concerned.

I am not suggesting that sawfly ecology is limited to a study of the ecology of the hostplant species. The distribution of a sawfly is by no means coincident with that of its hostplants; the hostplants will normally have a wider distribution, though individual hostplant species may be replaced by others locally or in wider areas; decisive factors such as minimum temperatures or humidities in critical stages of the sawflies' life histories are unlikely to be the same as those affecting the hostplant's survival or well-being; for sawflies, which are smaller than their hosts and mobile and with transient short stages, a micro-ecology comes into effect: their host may actually be

really but a small fraction of the whole hostplant—a bud, a fruit, a leaf-petiole, the underside or inside of a leaf and so on—with an ecology correspondingly but a small fraction of the whole plant's environment. What little is known of this will be considered in the Systematic Synopsis under the individual species.

Biogeography is actually ecology considered historically with phyllogeny and geography. It is dependent on unimpeachable taxonomy and systematics of living and fossil forms, and a correct interpretation of what geologists finally decide about past climates and geography. Our theories must be held in leash so as not to outstrip these truths.

A summary of what is now known about post-glacial conditions in Britain is given in the introductory chapters of Tansley (1939), and about the development and distribution of plant life through the ages in Seward (1933). The groundwork is not complete enough for us to start saying definitely where and when different groups of species (of sawflies) arose in the world and many of the conclusions of biogeographers such as Scharff (1907) and his disciples must be treated with the utmost reserve (but see Sections 4 (*e*), (*f*) and (*g*)).

Bristowe (1939) in discussing spider distribution points out that, despite the common argument that isolated tundra relics on our mountain tops date back to a tundra age when all these isolated faunas were linked by a common tundra, no one would postulate an age of caves or sandhills or ants' nests or marshes to explain away the distribution of animals common to any one of these isolated environments. But the different categories are not really comparable. The tundra fauna belongs to a broad climatic zone in the north, a major ecological climatic-climax area; the others are purely minor secondary divisions dependent on the effects of local conditions rather than climate. Furthermore, the differences between the isolated colonies are of rather a different order, the tundra being without such numerous intermediate stepping stones as must exist between marshes and sandhills.

Recent studies of the insect fauna of the upper air provide a plausible explanation for the present wide distribution of certain insects, especially minute ones; but, as suggested above, there seems little evidence that sawflies could be conveyed long distances this way and remain alive.

Starting, however, with the information now available about the distribution of sawfly species in Britain and Ireland we can recognize four main types of distribution, omitting obvious aliens.

(1) Arctic-alpine. Species limited mainly to the arctic conditions of our mountains.

(2) North-western. Species concentrated in Scotland, Ireland, Wales and northern England—that is to say, north or west of the

"highland line" of the geographers—and assumed to be associated with what corresponds to the northern and sub-alpine birch and coniferous climax forest type.

(3) Generally distributed. Species known to occur in the far north of Scotland (Caithness or Sutherland) as well as the Devonian peninsula and the south-eastern counties of England.

(4) Southern. Species limited to the area south-east of a line drawn from the Bristol Channel by way of the Severn, Avon and Trent to the Humber. This line approximates to the "highland line" of geographers which divides off to the north and west the mountainous area of hard palaeozoic rock outcrops, with its higher rainfall, less sun and more even, though lower mean temperatures (Tansley 1939, p. 9, fig. 4).

When we consider the distribution of these species outside Britain, bearing in mind the limitations to our knowledge already mentioned, we find that several of the species in group (1) are widespread arctic and alpine types, and that groups (2), (3) and (4) contain various distribution types. All these will be discussed in the next section.

Matthews (1937) following Salisbury (1932) has developed fine grades of distinction in dealing with the distribution of the British flowering plants *in Europe*. It does not, however, seem to me that in limiting their consideration mostly to the European distributions they have gone far enough, for important new distinctions begin to arise when the distributions outside Europe, especially in Asia, are also considered.

(*d*) Types of Palaearctic Distribution

As suggested in the previous section, a close correlation seems to exist between the Eurasian distribution patterns of sawflies and of flowering plants. When we study the distributions of our British sawflies outside Britain, we find that, where these are known, they fall into natural groups largely in accordance with the main Eurasian ecological zones (as shown in any general vegetation map) (cf. papers by Hultén on plants, Stegman on birds and Uvarov on grasshoppers).

(i) **Arctic tundra type** (Arctic or arctic-alpine tundra)

The species associated with the mountains in north and west Britain, have a Eurasian distribution concentrated in the arctic and alpine zones beyond or above the tree-line.

(ii) **Siberian type** (Subarctic-subalpine coniferous or taiga forest)

Several of our species, including many that are concentrated in north and west Britain, have a Eurasian distribution that is

concentrated in subarctic and subalpine zones where the coniferous or taiga forest is the climatic-climax, but which includes of course local phases of birch forest, bog or moor.

(iii) **European type** (Western palaearctic deciduous forest)

The majority of our species have a Eurasian distribution concentrated in the zone where the western deciduous mixed forest is the climatic-climax type.

(iv) **Mediterranean type** (Mediterranean scrub, heath and steppe)

A few species in southern Britain, including several that have been introduced with cultivated plants, are concentrated or probably had their origins in the Mediterranean region or the early centres of civilization in the E. Mediterranean.

(v–vii) **Mongolian, Chinese and Tibetan types** (Eurasian cold steppes, tropical, and mountain tundra)

It is not easy to separate the Mediterranean type from the species associated with the cold Eurasian steppes and some even apparently with Eurasian mountain tundra and scrub.

The placing of a species into its correct biogeographical type depends on a detailed knowledge of the species complexes and their ecological and geographical distribution on a world basis, knowledge that is rarely yet available in most groups. Rarely also is phylogeny sufficiently advanced for us safely to assume the exact relationship of units higher than subspecies. Thus though the species is generally the unit which must form the basis of our preliminary study, sometimes it may even be necessary to treat separately as species, units up till now regarded as of lower rank than species, such as "subspecies."

Unfortunately this is only the beginning of the troubles that ensue, for the general information given in standard works on distribution gives very little clue to the ecological distributions and preferences of the species. Many of the recorded geographical distributions could belong to more than one biogeographical type. Many of the named varieties may be distinct species or eco-geographical races of some kind with distinct distributions of their own. I have been guided to some extent by the recorded food-plants where any are known, working from the ecogeographical distributions of the foodplants where these could be discovered, bearing in mind that the sparse records of these often probably do not cover the full foodplant range of all the races of a sawfly species.

Without the necessary information, it is extremely difficult to separate all the Siberian from the European type when they all have a distribution known to be Eurasian, and Tibetan montane from Arctic types when so little is known about the sawfly fauna of Tibet,

and Mediterranean from European and Mongolian steppe types without a detailed knowledge of the fauna of Mongolia and other parts of Central Asia.

It is seen, therefore, that this approach is full of possible pitfalls where we have inadequate knowledge, and is impossible to apply accurately at present to every species. No attempt, therefore, is made to place every British sawfly into its biogeographical type, as on the basis of our present knowledge much of this would be too speculative to justify the expenditure of time involved. I make no apology for omitting altogether certain species whose published distributions might seem to fit them readily into one or other of the defined types. I have often preferred to err on the side of caution where I believe a more critical systematic analysis might reveal further important evidence.

Many of the sawflies that feed in Britain on cultivated plants (*Prunus*, *Pyrus* and *Rosa* of Rosaceae, *Onobrychis*, *Vicia* and *Trifolium* of Papilionaceae, *Rumex* and *Polygonum* of Polygonaceae, *Avena*, *Hordeum* and *Triticum* of Gramineae, etc.) are very widely distributed over Eurasia, some into N. America. Some of these have clearly spread from the early centres of civilization in the E. Mediterranean and S.W. Asia (see Benson 1935 (2)) where a large number of the cultivated food, medicinal or decorative plants had their centres of origin (see Vavilov 1940). Others of such sawflies are of more doubtful origin, but appear to be European, though it is not clear whether they are native British species or not (see Section 4 (*a*) (ii)).

Information on the extra-British distribution of British sawflies was taken primarily from the monograph of Enslin, the recent Catalogus Hymenopterorum (ed. by H. Hedicke) and the monograph by Gussakovskii so far as these go. These sources have been supplemented by data from any more recent systematic studies and from unpublished data on specimens in the British Museum. In addition to these sources the sawfly faunas of those areas which have been dealt with in recent faunistic papers have been specially considered as focal points, and card catalogues have been prepared for them. These include Lapland (Strand 1898, Malaise 1920-1 and 1931), Finland (Forsius and Hellén 1935), East Baltic (Conde 1927, 1934, 1937), East Siberia (Enslin 1927, Malaise 1931 (1), 1931 (2), Rohwer 1925, Takeuchi 1936, 1938, etc.), Asia Minor, Amanus Mountains (Fahringer and Friese), N. Iran, Elburz Mountains (Mallach 1931), S. Russian Steppes and N. Caucasus (Dovnar-Zapolskii 1931), Iberian peninsula (Dusmet 1932, Forsius 1927, 1930) and N. Africa (Forsius 1919).

Species marked with a "?" are referred with some doubt to the category concerned.

(i) **Arctic type (arctic and arctic-alpine tundra)**

This type has a wide, sometimes almost circumpolar, distribution in the arctic zone north of the tree-limit. Some elements occur discontinuously in the alpine zones of mountains that were connected with the arctic during the glacial period, such as the Pyrenees and Alps (but they do not reach the Caucasus or Tibet). (*See Figs.* 1 *and* 2.)

Floristically the zone is characterized by low shrubs and perennials with a short vegetative period.

In the sawflies the Arctic type (see Benson 1935 (1)) is represented mostly on the summits of mountains over 2,000 ft. in Scotland, in north England, down the Pennine Chain and in Wales, or at lower levels on river detritus brought down from mountains, and in west Ireland, and north and west Scotland at a few places almost at sea level. All belong to the subfamily Nematinae of the Tenthredinidae, except *Empria alpina* Benson and (?) *E. fletcheri* Cameron, and mostly they are associated with arctic species of *Salix* or *Vaccinium*. Distribution of these sawflies outside Britain is still so incompletely known that the different subdivisions of the type cannot be applied satisfactorily.

In general the arctic fauna and flora are centred in areas that during the maximal glaciation were north of the ice sheet or above it (Hultén 1937). They are subdivided into three groups:

(*a*) *Arctic.* Occurs in Arctic only.

(*b*) *Arctic-alpine.* Occurs in Arctic and also on tops of mountains linked with Arctic during glaciation.

(*c*) *Alpine.* Occurs now only on tops of mountains linked with Arctic during glaciation but extinct in Arctic proper. (Not to be confused with the Tibetan type which is centred in the montane zones of Asia, etc., never linked with the Arctic.)

The point about this classification is that only in E. Asia is there a link between the Arctic and the Alpine elements today (Hultén 1937).

Of these subdivisions we are only concerned here with the Arctic and Arctic-alpine.

(1) *Arctic-alpine species*

Species known to occur in the arctic zone of the mountains of Central Europe (where I found them in Valais, Switzerland, in 1935) as well as in arctic Europe.

Empria alpina Benson. (Mountains of Scotland, Upper Teesdale; as well as arctic and alpine Europe in general.)

Nematus (*Pteronidea*) *reticulatus* Holmgren (=*forsiusi* Enslin) (*Vaccinium*). (Mountains in Scotland and at Annagh Lake, Farnham in Co. Cavan, Ireland; also in arctic and alpine Europe generally and Spitzbergen, Bear Island and Novaya Zemlya.)

Fig. 1. Extreme Arctic Type: *Amauronematus abnormis* (Holmgren) (Scotland (Mt. Braeriach), Mountains of Lapland, Novaya Zemlaya, New Siberian Islands, Mouth of Lena River, and N. Behring Sound).

Fig. 2. Wide Arctic Type: *Pristiphora coactula* complex, which probably extends also into N. America and represents a general arctic-alpine range.

Nematus (*Pontania*) *femoralis* Cameron. (*Salix nigricans* Sm., *phylicifolia* L., *lapponum* L., etc.) (Mountains and higher river valleys in Scotland and Pennine Chain; arctic and alpine Europe generally.)

Pristiphora carinata Hartig. (Mountains of Scotland; arctic and alpine Europe generally.)

P. coactula Ruthe complex (*Vaccinium*). (Mountains and heaths in Scotland, and Pennine Chain to Cheshire, also summit of Gearhan, Cahercorree, S. Kerry, Ireland; Iceland and arctic and alpine Europe, N. Siberia to Kamtchatka.) (See Fig. 2.)

(2) *Arctic species*

Species not yet recognized as occurring in the Central European Alps and unless otherwise indicated not yet certainly known outside Britain.

Nematus (*Pontania*) *herbaceae* Cam. (*Salix herbacea* L.). (Mountains of Scotland, N. England and Wales, also in Lapland.)

N. (*P.*) *algidus* Benson (*Salix*? sp.). (Mountains of Scotland.)

N. (*Pachynematus*) *clibrichellus* Cameron. (Mountains of Scotland and Pennine Chain to Cheshire, sea coast in Caithness, Finland and N. America.)

Amauronematus abnormis Holmgren (? *Salix herbacea* L.). (Mt. Braeriach in Scotland, Mt. Snuoratjokko in Swedish Lapland, Finnish Lapland, Novaya Zemlya, New Siberian Islands, mouth of Lena River, and Behring Sound in N.E. Siberia.) (See Fig. 1.)

A. macluckiei Benson. (Mountains of Scotland and in Lapland.)

Pristiphora hyperborea Malaise (=*asperlatus* Benson) (*Salix herbacea* L., *nigricans* Sm., etc.). (Coast of Co. Mayo, Ireland, mountains of Scotland and N. England, Iceland, Lapland and E. Siberia.)

(3) *Widespread species of other types inhabiting British arctic zones*

The following widespread species of European type also inhabit the summits of our highest mountains: *Dolerus aeneus* Htg. (Gramineae) and *Empria liturata* Gmelin (Rosaceae); and various other species get carried up in wind-currents, but do not breed there.

In addition to these the following widely distributed species, probably of Siberian type, also inhabit the summits of our highest mountains.

Nematus (*Pachynematus*) *obductus* Htg. (Gramineae). (Generally distributed throughout Britain and Ireland as well as N. and C. Europe; also occurring in Greenland, Iceland, Faroes and Scandinavia to E. Siberia and (?) N. America.)

Pristiphora quercus Htg. (*Vaccinium*). (Widely distributed throughout Britain and Ireland, as well as N. and C. Europe to E. Siberia.)

P. mollis Htg. (*Vaccinium*). (Distributed as the preceding.)

(ii) **Siberian type (subarctic-subalpine coniferous or taiga forest type)**

This populates a continuous area in eastern Siberia and extends, with gradual reduction in the number of species, to the south Siberian mountains and those of northern Mongolia, as well as through the northern half of western Siberia into Scandinavia and Britain, and eastward into N. America. Siberian elements occur sporadically also into the subalpine forests of Central European mountains, the Pyrenees, a few to the Caucasus, and in Asia even to south-eastern Tibet. Characteristic of many of these species is that they extend further south in East than in West Europe. (*See Figs.* 3 *and* 4.)

Floristically the taiga or subarctic forest is about 30% evergreen with mainly conifers in the tree layer, but the conifers do not extend to the northern or alpine tree limit which is rich in *Salix* and *Betula*.

The Caledonian forest relics of Scotland are in the tree layer mostly of pine with birch, but of pure birch at the higher limits. Deforested areas may be dry heathland and, where the ground is too swampy for forest, will be marshy pastures, reedy moors or peat bogs. Our low-lying "taiga" is thus like that of western Siberia, without, however, such richness of species. This western taiga (Haviland 1926) is a mosaic of forest, meadows and swamps, and besides conifers and birches on the better drained land it is rich in sallows, alders and poplars. *Betula* is usually pre-climax to *Larix europeus* L. and *Pinus sylvestris* L.; and *Pinus sylvestris* L. to *Picea excelsa* L. It must not be forgotten, however, that *Pinus sylvestris* and other conifers are a normal constituent of the European deciduous forest on certain soils and their associated fauna is not necessarily of Siberian type (e.g. Crested Tit (*Parus cristatus* L.) among birds is of European type). In fact, several species with a British distribution limited to the north and west are nevertheless apparently of European type (see following chapter) and, on the other hand, most of the sawfly species of Siberian type are of general distribution in Britain.

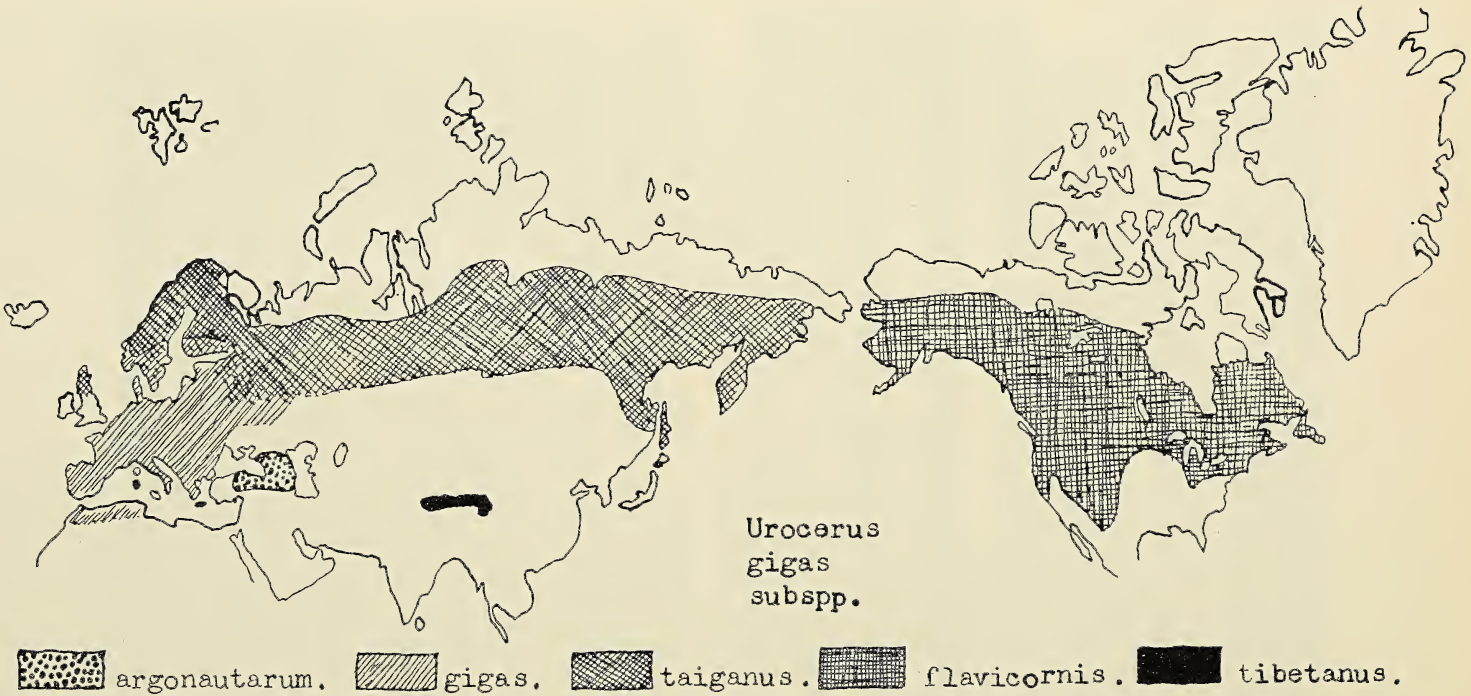

Fig. 3. Wide SIBERIAN and also EUROPEAN TYPE: *Urocerus gigas* subspecies: *taiganus*, *tibetanus* and *flavicornis* together representing a typical wide Siberian type of distribution; while *gigas* and *argonautarum* represent a typical European distribution.

Fig. 4. Wide Siberian Type: *Rhogogaster viridis* L.

To the taiga zone belongs most of the north and central Highlands except along the lowest zones of the deepest glens where oak-wood occurs. The zone also extends south-westwards along the Atlantic side of Scotland, Wales and Ireland, and above the deciduous forest in south Scotland, north England and south-westwards through Wales even to Dartmoor; but with birch-wood, without conifers, or else heathland, as the climatic-climax type. In general (except near the Atlantic) this fauna and flora occupies land now that was covered by the Ice sheet during the maximal glaciation; near the Atlantic (e.g. in Britain) it has retreated northwards or been mingled with the advancing European fauna and flora (Hultén 1937).

It seems that many species have a distribution that is European as well as Siberian. In a few cases we are beginning to recognize that this is due to the confusion between paired subspecies, one of which has a European and the other a Siberian distribution, and it is almost certain that this will later be recognized in many more species. Paired subspecies of this kind have been recognized in Britain in *Pamphilius hortorum* Klug. *Urocerus gigas* L., *Arge fuscipes* Fallén and *Dolerus germanicus* F.: the Siberian one confined to the north and west, and the European one confined to the south (see Benson 1945 (1)). In many other species, mean differences occur in Scotch (Siberian) and English (European) populations, but the subspecies are less easy to define: this often seems to be due to the blending of a European and a Siberian race in north Europe. Many of the species listed may also contain subspecies groups that are European in distribution and it may prove, especially with those with a southern British distribution, that the Siberian group of subspecies is not actually present in Britain.

The following British sawflies, besides occurring in North and Central Europe, extend their ranges right across Siberia to the Pacific coast and many of them, at least in part, probably belong to the taiga fauna.

Some of those listed below in groups (1) and (3) may really, therefore, belong partly or entirely to European group (2).

(1) *Species attached to coniferous trees*

Xyela julii Breb. (*Pinus*. Widespread in Britain and Ireland but concentrated in Caledonian forest. Replaced by related species in S. Europe.)

Acantholyda erythrocephala L. (*Pinus*. Restricted in Britain to Caledonian forest. Reaching in S.E. Europe to Caucasus.)

A. posticalis Matsumura. (=*pinivora* Enslin) (*Pinus*. Restricted in Britain to Caledonian forest.)

Urocerus gigas taiganus Benson. (The usual Scottish form is probably a hybrid between the Siberian *U. gigas taiganus* Benson and the W. European *U. gigas gigas* L. (see Benson 1943 (2)). The latter is a common British introduced alien; the former is probably native in Scotland. (See Fig. 3.))

Gilpinia virens Kl. (*Pinus*. Occurs in Britain in Caledonian forest, also as introduction in S. England. To Spain in W. Europe.)

[? *G. hercyniae* Htg. (*Picea*. S. England. Alien.)]

Neodiprion sertifer Geoffroy. (*Pinus*. Throughout Britain and Ireland, mostly by introduction, but probably native in Scotland.)

(2) *Species attached to angiosperm trees and shrubs*, and already recorded as occurring in Kamtchatka or other parts of E. Siberia. Unless otherwise indicated they have a wide or even general distribution in Britain.

Pamphilius pallipes Zett. (*Betula*.)

P. stramineipes Htg. (*Rosa*. In Britain restricted to Scotland.)

P. varius Zett. (*Betula*.)

P. inanitus Villier. (*Rosa*.)

P. histrio Latreille. (*Populus*.)

P. hortorum bicinctus Benson. (*Rubus*. Restricted to Scotland and Scandinavia; in S. England replaced by the European *P. hortorum hortorum* Klug).

Xiphydria camelus L. (*Alnus* and *Betula*. England, Wales and Scotland, but (?) not Ireland. In E. Europe to Asia Minor.)

Arge enodis L. (=*coeruleipennis* Retz). (*Salix*, England.)

A. ustulata L. (*Salix* and *Betula*.)

A. nigripes Retz. (=*enodis* L. auct.). (*Rosa*. England.)

A. gracilicornis Klug (=*coerulescens* Geoffroy). (*Rubus*.)

A. metallica Kl. (*Betula*. Ireland.)

Arge fuscipes expansa Klug. (*Betula* and *Salix*. Restricted to N. Britain and Ireland and replaced in S. England by the European *Arge fuscipes fuscipes* Fall.)

Sterictophora geminata Gmel. (*Rosa*.)

Cimbex lutea L. (*Salix*.)

Trichiosoma lucorum L. (*Betula*, *Crataegus*, etc.)

T. vitellinae L. (*Salix*. Throughout Britain but (?) not Ireland.)

Zaraea fasciata L. (*Lonicera*, etc.)

Tenthredo ferruginea Schrank. (*Salix*, *Prunus*, *Spiraea*, *Pteris*, etc.)

T. colon Klug. (*Salix*, *Circaea*, *Epilobium*, *Pteris*, etc. To Asia Minor.)

Rhogogaster viridis L. (*Salix*, *Betula*, *Alnus*, etc. Spread over W. of N. America.) (Fig. 4.)

R. chlorosoma Benson. (*Salix* and *Alnus*.)

Allantus cinctus L. (*Rosa*.)

A. basalis Klug. (*Rosa*. Restricted to Scotland and in an endemic form, *A. basalis caledonicus* Benson.)

? *A. cingulatus* Scopoli. (*Rosa*. S. England to Yorks.)

Ametastegia albipes C. G. Thomson. (*Salix* and *Populus*. England and Ireland.)

Empria candidata Fallén. (*Betula*.)

E. immersa Kl. (*Salix*.)

?*Blennocampa pusilla* Klug. (*Rosa*.)

Fenusa pusilla Lep. (*Betula*.)

?*Caliroa annulipes* Kl. (Various trees as well as *Vaccinium*.)

Cladius pectinicornis. (*Rosa*. To Iberian peninsula and Asia Minor.)

Trichiocampus viminalis Fallén. (*Populus* and *Salix*. To N. America.)

Priophorus tener Zadd. (*Rubus*. To Caucasus.)

P. varipes Lep. (=*padi* auctt.). (Various rosaceous trees and *Betula*. To Caucasus and Trans-Caucasia, but not Asia Minor.)

Hemichroa crocea Geoffroy. (*Alnus* and *Betula*. To N. America (?) introduced.)

Dineura testaceipes Klug. (*Pyrus aucuparia* L. N. Britain and Ireland. To Caucasus.)

Dineura viridorsata Retzius. (*Betula*.)

Nematus (*Euura*) *amerinae* L. (*Salix pentandra* L. Chiefly in N. England and S. Scotland. In C. Europe also on *Populus*.)

N. (*E.*) *saliceti* Fallén. (*Salix*.)

N. (*Pontania*) *apicifrons* Malaise. (*Salix pentandra* L. N. Britain.)

N. (*P.*) *anglicus* Cam. (*Salix viminalis* L.)

N. (*P.*) *leucapsis* Tischbein. (*Salix caprea* L., *aurita* L., *atrocinerea* Brot., etc.)

N. (*Pontania*) spp.; probably several others in this subgenus.

N. (*Pteronidea*) *ferrugineus* Förster. (*Salix*.)

N. (*Pt.*) *miliaris* Panzer. (*Salix*. To Asia Minor.)

N. (*Pt.*) spp.; probably several others of this subgenus.

N. (*Pachynematus*) *vagus* F. (*Salix* and *Carex*.)

N. (*Holcocneme*) *crassus* Fallén. (*Salix*, *Populus*, *Betula* and *Rumex*.)

Amauronematus histrio Lep. (*Salix*. To Caucasus.)

A. fallax Lep. (*Salix*. Mostly north Britain and Ireland. To Caucasus.)

A. humeralis Lep. (*Salix*. Britain.)

Amauronematus spp.; probably several others of this genus.

Nematinus acuminatus C. G. Thomson. (*Betula*.)

N. caledonicus Cameron. (*Betula*.)

Pristiphora geniculata Htg. (*Pyrus aucuparia* L. England and Ireland.)

P. punctifrons C. G. Thomson. (*Prunus* and *Rosa*. To Iberian peninsula.)

P. ruficornis Olivier. (*Crataegus*, etc. To Caucasus and Asia Minor.)

Pristiphora spp.; probably several others of this genus.

(3) *Other species including many associated with bogs and recorded from Kamtchatka or other parts of E. Asia.*

Arge ciliaris L. (*Filipendula ulmaria* L.)

Tenthredo mesomelas L. (*Polygonum*, *Arctium*, etc.)

T. velox F. (N. Britain only.)

T. olivacea Klug. (Throughout Britain but apparently absent from Ireland.)

Pachyprotasis variegata variegata Fallén. (*Solanum tuberosum* L., *Digitalis*, etc.) (*P. v. brunettii* Rohwer in Himalayas and *P. v. tenebrosa* Malaise in Kurile Isles.)

P. simulans Klug. (*Solidago* and *Scrophularia*.)

P. antennata Klug. (*Filipendula* and *Fraxinus*.)

P. rapae L. (*Betonia*, *Fraxinus*, *Scrophularia*, etc.)

P. nigronotata Kriechb. (*Plantago*.)

Loderus eversmanni Kirby (=*palmatus* Klug). (*Equisetum*.)

L. pratorum gilvipes Kl. (*Equisetum*. Restricted to N. Britain; replaced by the European *L. pratorum pratorum* in S. England.)

Dolerus germanicus fuscipennis Stephens. (*Equisetum*. The Scottish and north Scandinavian *D. germanicus fuscipennis* Stephens is closely related to the E. Siberian *D. germanicus orientalis* Zhel., etc. In England this is replaced by the European *D. germanicus germanicus* F.)

D. cothurnatus Lep. (*Equisetum.*)

D. saxatilis Htg. (*Equisetum.* N. Britain to Staffordshire, all British forms belonging to an endemic British melanic race: *D. saxatilis scoticus* Cameron.)

D. gessneri C. G. Thomson. (*Equisetum.* N. Britain, S.W. to Gloucester and in Ireland.)

D. nitens Zaddach. (Gramineae (?). Also in N. America.)

D. asper Zaddach. (*Carex.* To Caucasus.)

Allantus truncatus Kl. (*Filipendula, Fragaria,* etc.)

Protemphytus perla Kl. (*Polygonum.*)

P. pallipes Spin. (*Viola.* To Iceland and N. America.)

P. carpini Htg. (*Geranium.* To Iberian peninsula.)

Eutomostethus punctatus Konow . (*Carex.*)

Stromboceros delicatulus Fallén. (Filicales.)

Strongylogaster mixta Kl. (Filicales. Mostly N. Britain, also in Ireland.)

Aneugmenus temporalis C. G. Thomson. (Filicales.)

A. coronatus Kl. (Filicales.)

Melisandra morio F.

Nematus (*Pachynematus*) *umbripennis* Eversmann. (*Carex.*)

Nematus (*P.*) *obductus* Htg. (*Gramineae.* To Faroes, Iceland and Greenland, and (?) N. America.)

Pristiphora mollis Htg. (*Vaccinium.* N. Britain and Ireland.)

P. quercus Htg. (*Vaccinium* and *Betula.*)

(iii) **European type** (Western palaearctic deciduous forest).

Connected with the western Europe deciduous forests, and extending continuously, but in a gradually narrowing zone, to the southern Urals. Many species belonging to this type penetrate into northern Europe and south-western Siberia, while some occur sporadically north-westward into N. America and eastwards into S. Siberia and beyond. The forests of North Africa are also populated largely by this type, so are the forests of the Caucasus and Turkestan. (*Figs.* 3, 5 *and* 6.)

Forests belonging to this type are the normal climatic-climax of most of Britain and Ireland except in the north, north-west and on the mountains. Oaks are the natural predominant climax-trees of most of central and southern Britain; in the shallow limestones these give place to ash in the north and west, and to beech in the south-east; beech also ousts oak in the south-east on the loams and clays overlying the chalk.

Fig. 5. Wide EUROPEAN TYPE with endemic British subspecies: *Arge pagana* Panzer.

Pre-climax to oak-wood are heaths, with or without birch, giving place in the wetter places to climax bogs or alder-wood, most prominent in the fenland alder-carr and in the more exposed places, particularly on the Atlantic seaboard, to climax heaths where oceanic elements of the Mediterranean type intermingle with the European type. Grassland is probably not a climatic-climax in Britain, except on the more exposed limestone hills, such as perhaps on the chalk of the North and South Downs and the Chilterns, and almost certainly on the carboniferous limestones of the Pennines, Wales, the Mendip Hills in Somerset and extensively in Ireland.

Conifers other than *Juniperus* and *Taxus* are not apparently a normal or at least surviving endemic constituent of the deciduous forest in southern Britain as they are in central and southern Europe, though, when introduced into England, *Pinus* reproduces itself to form sub-spontaneous pinewoods on the south-eastern heaths.

The greater part of the British fauna and flora belongs naturally to the European type and many of Salisbury's (1932) finer grades of European floral distribution belong in part to this type.

In general this flora and fauna are associated with land that was south of the ice sheet during maximal glaciation though near the Atlantic (e.g. Britain) it has advanced northwards and mingled with the taiga fauna (Hultén 1937).

Many of the European type of sawflies on the one hand penetrate the subarctic and subalpine taiga, and on the other the steppes of south-east Europe or maquis of the western Mediterranean. Many of the species peculiar to Europe belong to this type, not only those associated with the various kinds of climax or subclimax deciduous forest, but also those peculiar to European coniferous forests (cf. the Crested Tit (*Parus cristatus* L.) among birds).

The typical European type of sawflies is shown by such species as: *Tenthredo maculata* Geoffroy (all Europe with Caucasus and Asia Minor); *Periclista albida* Kl., etc. (*Quercus:* N. and C. Europe to Caucasus): characteristic also of European type is the division into western (Atlantic) and eastern (Continental) forms whose ranges, since the retreat of the glaciers, have met again in C. Europe (and Britain), e.g. *Pristiphora denudata* Konow and *P. pallidiventris* Fallén (see 4 (*e*) (iii)).

(1) Species of European type attached to *Pinus sylvestris* L. and other conifers include:

Diprion pini L. (*Pinus.* In Britain apparently native in the Caledonian forest and introduced elsewhere.)

[*D. simile* Htg. (*Pinus* as introduction in S. England. A species belonging to the subalpine forests of Central Europe.)]

Fig. 6. Disjuncted EUROPEAN TYPE with two subspecies: *Macrophya* 12-*punctata* L.: (*a*) 12-*punctata* L.; (*b*) *sodalitia* Mocsáry.

Gilpinia pallida Kl., *G. frutetorum* F., and *Microdiprion pallipes* Fallén. (All on *Pinus* and in Britain confined as natives to the Caledonian forest and in Europe to subalpine and northern regions.)

Monoctenus juniperi L. (*Juniperus*. In Britain confined to Spey Valley (cf. Crested Tit) and to northern and subalpine Europe.)

[*Anoplonyx duplex* Lep. (*Larix*. Central and north Europe to west Siberia. Introduced into Britain.)]

[*Nematus* (*Pachynematus*) *imperfectus* Zaddach and *Pristiphora laricis* Hartig. (*Larix*. Central and N. Europe, and introduced into Britain.)]

[*Nematus* (*Pachynematus*) *scutellatus* Hartig and *montanus* Zaddach, *Pristiphora abietina* Christ., *P. ambigua* Fallén and *P. compressa* Hartig. (*Picea*. Central and N. Europe, and introduced into Britain.)]

[cf. *Urocerus gigas* L. Fig. 3.]

(2) Species, from available information, apparently showing disjunction into two isolated or narrowly connected provinces in (*a*) Europe and (*b*) Maritime Siberia, Japan or China.

Some of these may really be more widely dispersed into the taiga and prove to belong entirely or in part to the Siberian type; likewise some listed above as of Siberian type may belong here entirely or in part. Where the eastern form is separated as a distinct subspecies the name of the subspecies is included in brackets.

Neurotoma saltuum L. (=*flaviventris* Retz). (*Crataegus*, *Pyrus*, *Prunus*, etc.)

[*Blasticotoma filiceti filiceti* Klug. (Filicales.) (*B. filiceti pacifica* Malaise.)]

Tenthredo temula Scop.

T. atra L. (*Lamium*, *Mentha*, *Plantago*, *Ranunculus*, etc.)

T. fagi fagi Panzer. (*Pyrus aucuparia* L.) (*T. fagi facigera* Konow.)

Tenthredopsis nassata L. (Gramineae and other herbaceous plants.)

Macrophya duodecimpunctata duodecimpunctata L. (*Carex* and Gramineae.) (*M. d. sodalitia* Mocs.) (Fig. 6.)

M. annulata Geoffroy.

Dolerus pratensis pratensis L. (=*dubius* Klug). (*Equisetum*.) (*D. pratensis variator* Enslin.)

Athalia lugens lugens Kl. (Cruciferae.) (*A. lugens imfumata* Marlatt, etc.)

A. cordata cordata Lep. (*Ajuga*, *Lycopus*, *Veronica*, etc.) (*A. cordata kashmirensis* Benson, etc.)

A. lineolata Lep. (*Nepeta, Arctium, Plantago*, etc.)

A. rosae rosae L. (=*colibri* Christ.). (Cruciferae. Extends to E. Siberia, Japan and N. China; replaced in S. China and India by *A. rosae leucostoma* Cameron.)

A. liberta Klug. (*Ajuga, Veronica, Sisymbrium*, etc.)

Allantus togatus Panzer. (*Quercus.*)

Tomostethus nigritus F. (*Fraxinus.*)

Eutomostethus punctatus Konow. (*Carex.*)

Heptamelus ochroleucus Haliday. (Filicales.)

Strongylogaster filicis Klug. (Filicales.)

S. lineata Christ. (Filicales.)

(3) *Species with an Atlantic distribution:*

Pristiphora denudata Konow. (Azores, Madeira, Spain, France, W. Germany and England; closely related to *C. pallidiventris* Fallèn which occurs throughout Britain and Ireland, North, Central and South-east Europe to Caucasus. Probably these two should be regarded as once isolated geographical subspecies now meeting on a broad front.)

Zaraea lonicerae L. (S. Britain, France and Holland; very closely related to *Z. aenea* Klug of C. and E. Europe and Scandinavia, though it too reaches S. Britain.)

(See discussion in Section 4 (*e*) (iii) and cf. *Elinora flaveola flaveola* L. and *f. dominiquei* Konow of Mediterranean type, and also *Sciapteryx soror* Konow and *S. costalis* (F.) of (?) Tibetan type.)

(iv) **Mediterranean type** (Mediterranean scrub, heath and steppe).

Species associated with the xerophilous scrubs, heaths and steppes of the Mediterranean region, and south-western Asia. In Europe they extend northwards into the Hungarian Plain, Germany and even a few into Britain and Scandinavia, while the more oceanic elements extend up the Atlantic coast to Britain and Ireland. Southwards some of the species extend into the East African mountains. (*Figs.* 7 *and* 8.)

Haviland (1926, p. 131) points out that the dry steppes and semi-deserts of Eurasia possess a rich semi-aquatic or lacustrine fauna centred round lakes and rivers, and that the birds characteristic of this area are often specifically identical with our original peculiar fenland and dwindling marsh avifauna with its bitterns, rails, herons, avocets, ducks, harriers, etc. The rich semi-aquatic fauna of the dry steppes has thus its counterpart in our fenlands, close to the dry steppe-like Breckland of East Anglia, with its steppe and

Fig. 7. MEDITERRANEAN TYPE: *Elinora* spp.

marsh relics of Mediterranean and Eurasian origin. The sandy soil of the Breckland and the more continental type of climate there than anywhere else in Britain provide the chief refuge for several southern continental and steppe species (e.g. of flowering plants, see Salisbury (1932) or Tansley (1939, p. 512), while others survive on the quick-drying chalk downs of S.E. England.

Mediterranean elements favouring an oceanic climate spread up the Atlantic fringe even into Scandinavia. The Atlantic climatic-climax heaths and scrubs of southern Ireland, south-west and southern England contain various of these Mediterranean elements (e.g. in plants, the Strawberry Tree (*Arbutus unedo* L.) and several other Ericaceae, etc.), some of which penetrate the subclimax heaths of cleared forest.

Mediterranean sawflies in Britain include the following; several of them are attached to cultivated plants and these almost certainly had their origin in early centres of civilization in the E. Mediterranean.

Cephus pygmaeus L. (Corn Sawfly, on wild and cultivated Gramineae. England and Wales; throughout Europe to N. Africa, Palestine, Caucasus, N. Persia and Turkestan.)

Trachelus tabidus F. (On wild and cultivated Gramineae. England S.E. of Humber/Severn line and Glamorgan. Throughout Europe to Algiers, Egypt and Asia Minor.)

Sterictophora furcata Vill. (*Rubus*. S. England to Durham, but very scarce. C. Europe to N. Africa and Asia Minor; concentrated in S. where occur three other related species.)

Elinora flaveola dominiquei Konow. (*Sinapis* and *Bupleurum*. Rare in S. England; Spain and France. Genus concentrated in W. Mediterranean. (See Figs. 7 and 8.))

[Probably many of the yellow-banded short-horned *Tenthredo* belong to the Mediterranean or the Eurasian steppes as they are characteristic of flowery pastures and not woodlands, are in England concentrated S.E. of Humber/Severn line and in Europe in the Mediterranean and S.E. On the contrary the long-horned *Tenthredo* are typical woodland and forest insects (European and Siberian types). *Tenthredopsis* and the graminivorous section of *Dolerus* are also characteristic steppe insects and some of our representatives of these genera may belong here.]

Athalia bicolor Lep. (*Veronica*, *Sisymbrium*, etc. England mostly S.E. of Humber/Severn line. All Europe, N. Africa, Asia Minor and Trans-Caucasia. This and the following species belong to a section of the genus concentrated in the E. Mediterranean.)

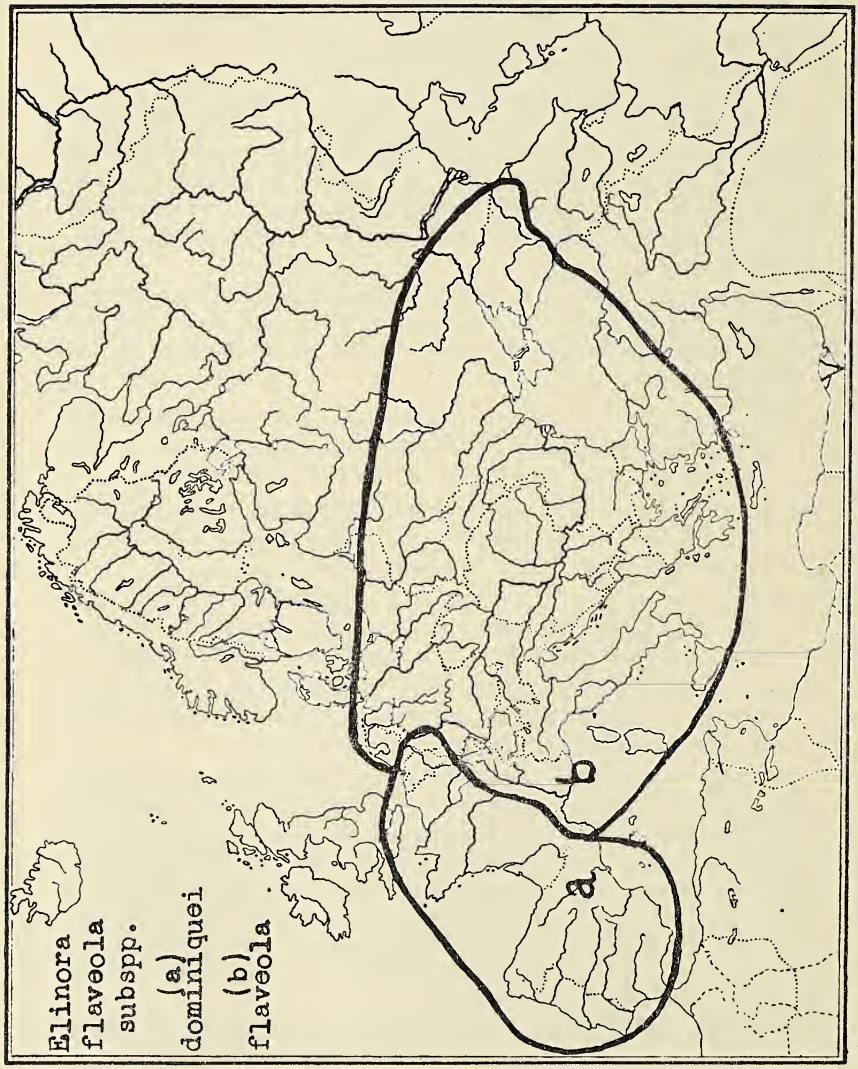

Fig. 8. Mediterranean Type with Atlantic and continental subspecies: *Elinora flaveola* (Gmelin).

A. glabricollis Thomson. (Cruciferae. Throughout Britain. All Europe to N. Africa, Caucasus and Asia Minor.)

? *Caliroa limacina* Retz. (Cultivated *Pyrus* and *Prunus* and many other trees and shrubs. Throughout Britain and Ireland; introduced to almost all parts of the world where pears, cherries and plums are grown.)

[*Hoplocampa flava* L. (*Prunus*, mostly cultivated forms. In Britain mostly in S. England. C. Europe to Caucasus and Asia Minor. Here also possibly belong *H. testudinea* Klug (*Malus pumila* Miller) and *H. brevis* Klug (*Pyrus communis* L.), which have probably been carried by man from the E. Mediterranean.)]

(v - vii) **Other types (Mongolian, Chinese and Tibetan)**

In Europe there also occur three other of Stegman's Distribution Types, though they have not yet for certain been recognized among British sawflies:

(v) *Mongolian type.* This is characteristic of the steppes and cold deserts of Mongolia and among birds is represented in this country by the chough and twite. Many of the so-called steppe plants belong not here at all but merely to a continental branch of the European type.

(vi) *Chinese type.* This represents the characteristic fauna and flora of the mixed forests of S. Japan and S.E. Asia from China to Indo-Malaya.

(vii) *Tibetan type.* This is characteristic of the alpine zone of Tibet, the Himalayas and other mountains of C. and S.W. Asia with the Caucasus that were never connected with the Arctic during Pleistocene Glaciation. Among birds the Rock and Water Pipits and the Black Redstart belong here.

Sciapteryx soror Konow (? *Ranunculus*) probably belongs here, for though it has an entirely Atlantic European distribution it belongs to the *Sciapteryx costalis* complex which is centred in the Caucasus, the highlands of Turkestan and Tibet; and though these are species of very early spring in our latitudes, the genus nowhere reaches the Arctic (Fig. 9).

4 (*e*) Origin of Biogeographical Types in Britain and Ireland

It seems unlikely that representatives of any of these biogeographical types other than Arctic and perhaps a few northern representatives of the European and Siberian types could have survived through the whole of the Quaternary Glacial period within the present boundaries of Britain and Ireland, for during the major phase of glaciation (Riss) most of Britain north of the Thames and Severn, and Ireland except the extreme south-west was ice-covered.

Fig. 9. Range of known *Sciapteryx* spp.: possibly Tibetan type as the C. Asian montane fauna is scarcely explored yet.

It was during this major phase of glaciation that Lindroth (1935) postulates that the interchange between the alpine and arctic fauna and flora took place in the plains of Central Europe. To deny that Europe had necessarily an arctic climate during the Riss phase would entail some other explanation of this interchange. It might, for example, have taken place in E. Asia where mountain ranges reach up into the Arctic (cf. Hultén 1937).

Following the major glacial phase two warm interglacial and two minor glacial phases of less and less intensity succeeded. Various European and Siberian species may have survived in Britain and Ireland through these minor glacial phases. It would appear that most of the sawflies with a general or south-eastern British distribution are entirely post-glacial in their migration here.

Beirne (1943) argues that those Lepidoptera with a restricted and discontinuous distribution in the west and north of Britain (often with endemic races) entered these islands before the last minor glacial phase and he includes among these the Atlantic and "Lusitanian" elements of European and Mediterranean type.

Since England was not finally severed from the European continent until late Atlantic times, it would appear that the post-glacial land-bridge across the English Channel could have provided a passage for all the present ecological types in Britain (see Tansley 1939). For the climate fluctuated during this period from the immediately post-glacial sub-arctic conditions: through the warm-dry Boreal period (warmer than today) when Mediterranean and other steppe types could have entered Britain; through the warm-wet Atlantic period when the "Lusitanian" and other oceanic representatives of the European or Mediterranean type could have spread northwards across western France and found their way to their present refuges in the south-west before England was severed from the continent. Here they would have become restricted by the cool dry sub-Boreal period to follow (Tansley 1939). The time of the final breakdown of the last land connection with Ireland is of course fundamental in discussing this question. Should it be found that the bridge was broken down much before the onset of the warm-wet Atlantic period, then some other explanation than the one given above is needed to account for the presence of these south-western species in Ireland.

Of the Siberian type it is perhaps significant that those sawflies associated with marsh and bog, or with birch and willow, are remarkably well represented in the British fauna, but that the conifers and their associated fauna are poorly represented. This can be explained by remembering that the vanguard of the Siberian (taiga) immigrants, the first able to cross the marshes of the disappearing Ural Sea would be marsh and bog species; these

together with those attached to the northern taiga fringe of willow and birch, may well be interglacial or even pre-glacial in origin, or, if post-glacial, they could the more easily cross the Dogger Bank bridge of sub-arctic or Boreal times (Lindroth 1935) which from its very nature apparently excluded the passage of the drier taiga forest types (note that neither *Picea* nor *Larix* were able to cross this bridge in post-glacial times). Furthermore, this Dogger Bank bridge was presumably our last link with the continent when a swollen River Rhine flowed down the English Channel.

In fact it would appear that the Siberian taiga seems to be represented in Britain and Ireland mostly only by its northern willow-birch fringe together with heath and bog, the Caledonian and Central European coniferous forests being mostly but local developments of the European mixed forests (note also that the Crested Tit (*Parus cristatus* L.) is of European and *not* of Siberian type).

(*f*) British Endemic Elements

I shall not attempt to deal here with species described from British material as the result of recent critical systematics and not yet looked for elsewhere. Nor shall I deal with those "species" which show more variation in other parts of their range than in Britain (morphological or biological); the status of these exotic forms is unknown; their presence may indicate differences in genetic constitution or the existence of additional unrecognized species.

We have, however, a few insular races of well-known European species; these could probably be multiplied by comparisons between representatives of other species from Britain and continental Europe, on an absolute basis or by statistical means of populations, but we shall still be far from discovering whether the differences are genetic or environmental or a combination of the two. I will give one or two clear examples.

Arge pagana Panzer subsp. *stephensii* Leach (see Fig. 5). The British form of this species, limited to southern England, is paler than the continental form. In this British form the wings are subhyaline, and yellow marks appear on the tibiae, femora and more or less on the mesopleura and even mesonotum. One characteristic of this subspecies is its great variability in colour pattern. The typical continental form, occurring throughout Central Europe, southern Scandinavia and across Siberia to Kamtchatka, has the legs, mesonotum and mesopleura entirely and invariably black, and the wings heavily infuscate. The real status of the British form is unknown but provisionally I regard it as a geographical subspecies. It is very interesting that Britain should have an insular form paler than that on the continent, when most of our other observed insular forms (of sawflies) are darker.

Dolerus saxatilis Htg. subsp. *scoticus* Cameron.

This species is widespread and locally abundant on *Equisetum* in Scotland and north England. Our species is mostly entirely melanic in the Highlands and north of England, having only rarely (*c.* 1 : 100) any sign of a red band on the abdomen and only the front knees of the legs red. For this reason it was formerly considered to be a distinct species and was only recently identified as being a race of the boreal and subalpine Eurasian *D. saxatilis* Htg., which throughout the mainland of northern Europe and Siberia has a red-banded abdomen and at least red tibiae to all the legs. The British form, however, retains the pale hyaline wings, which distinguishes the species from most of its relatives; it has become melanic only in its body and legs. In Kamtchatka, however, all stages between entirely melanic to red-banded forms occur in mixed populations.

Now, when I was at Thurso in 1935 I discovered that the colonies I found up there differed from the Highland forms by having the front tibiae almost entirely red! More recently among specimens I have seen from Cheshire and Staffordshire there appears to be a somewhat higher proportion of red-marked forms. The genetic status of our race has not been studied; but it appears that a melanic mutation such as has arisen in several other insects, notably, for example, in the single-gene melanic mutation of the Peppered Moth (*Biston betularia* L.), has perhaps spread out from a centre in southern Scotland and has not yet entirely swamped the populations in the extreme northern and southern parts of its range. In the moist oceanic climate of Kamtchatka a remarkably similar melanic form occurs, but only as an extreme variety in a very variable population, of which the majority are yet of the normal red-banded red-legged form (a condition similar to that existing today in British populations of *D. pratensis* L.).

Dolerus germanicus F. and *Loderus pratorum* Fallén both occur in Britain with a melanic Siberian race in the north but a normal European race in the south; other species have numerous melanic forms appearing apparently at random throughout their ranges (*D. pratensis* L.) or as rare aberrations (*D. madidus* Klug); still others are normally melanic with occasional red-banded forms throughout their range (*D. gessneri* Ed. André): *Dolerus sanguinicollis* Klug and *megapterus* Klug are melanic in Britain, but in Central Europe also occur with forms with a more or less red-marked thorax.

Croesus septentrionalis L.

In Ireland an entirely black form of this species has been found more than once. The form has not been recorded from elsewhere, although entirely black related species occur in N. America and the Himalayas.

Mr. Stelfox sent some of the black Irish specimens to Dr. Perkins, who, by breeding, found that the black form acted as a simple Mendelian recessive to the normal red-banded form.

(*g*) Ecological Origins of Sawfly Groups

It seems likely that many groups of sawflies arose in the Mesozoic coniferous forests of the northern hemisphere. By analysing all the known foodplants of sawflies I have been able to show that a large majority of genera are today attached to families of plants predominantly arborescent rather than herbaceous (using Hutchinson's classification 1926).

This is so in the sawfly families Xyelidae, Pamphiliidae, Syntexidae, Xiphydriidae, Siricidae, Cephidae, Orussidae, Cimbicidae, Pergidae, Argidae, Diprionidae and Tenthredinidae; all in fact except the Megalodontidae and Blasticotomidae.

Where, in a group, some are attached to herbaceous plant families and others to arborescent, it is often clear that those attached to the arborescent plants are the more primitive (Cephidae, Argidae, Cimbicidae and (?) some subfamilies of Tenthredinidae). Some families are entirely attached to coniferous trees (Syntexidae and Diprionidae); while in others, which include both coniferous and angiospermous foodplants, those attached to conifers are clearly more primitive than those attached to angiosperms (Cephalciinae versus Pamphiliinae, etc., in Pamphiliidae (cf. Benson 1945 (2)), Siricinae versus Tremicinae in Siricidae (cf. Benson 1943 (2)), and the very archaic Australian *Zenarge turneri* Rohwer, attached to the coniferous *Callitris* (Cupressaceae), versus all the other Argidae). A possible exception to this general rule appears to be in the Xyelidae; the two genera *Megaxyela* and *Macroxyela* are, so far as is known, attached to angiosperm trees, but, having orthandrious male genitalia, must surely be regarded as more generalized than the genera *Xyela* and *Pleroneura* with inverted (strophandrious) genitalia and attached to conifers. But it must be remembered that the earliest fossil sawfly (and earliest fossil hymenopteron) *Liadoxyela* is a lower Jurassic form, surely of pre-angiosperm age.

It appears then that at least the families Xyelidae, Pamphiliidae, Syntexidae, Siricidae and Diprionidae were closely associated with the northern coniferous forest in their development; they do not today cross over into the southern hemisphere except in the far east, and their history is probably bound up with that of the northern temperate and boreal forest with which they have remained associated. The Megalodontidae and Blasticotomidae are also entirely northern, and the following are predominantly northern: Cephidae (except for the Athetocephinae in Madagascar), and of the Tenthredinidae, the Nematinae (except for a few species in the mountains of South America and in the Indo-Malayan region), the

Tenthredininae (except for a few primitive genera in South America and several genera in the Indo-Malayan region), the Dolerini of the Selandriinae (except for the high mountains of East Africa), and the Heterarthrinae. Sawflies of the southern hemisphere, apart from these exceptions, belong to the following groups common to the northern hemisphere: Orussidae, Xiphydriidae, Argidae, and Tenthredinidae of the subfamilies Selandriinae and Blennocampinae, and the large family Pergidae, entirely confined to Australia and South America (save for a few invaders into North America) and, so far as is known, predominantly attached to the arborescent Myrtaceae.

Some of the European groups, such as the fern-feeding Selandriinae, for example, represented by 12 species in Britain, have their vast hordes of nearly related species and genera in the Neotropical and Oriental regions, probably likewise attached to ferns. Our Blennocampinae (mostly on arborescent plants or monocotyledons) show a similar distribution and proportion. There is nothing unusual in this, for, as Stegman (1932) points out, the taiga flora was directly derived from an impoverished warm tertiary flora; 30% of the taiga flora today is evergreen and many of the typical species, such as the Vacciniaceae and Ericaceae, belong to essentially tropical families of plants.

The Tenthredininae, although scarcely represented in S. America or Africa, have numerous species belonging to our genera and nearly related genera in the Oriental region, and probably arose there.

The European Argidae, Cephidae, Cimbicidae and Megalodontidae all show a rich endemic Mediterranean development, but each of these families has a different world distribution: the Argidae are world-wide; the Cephidae are entirely northern, except for Madagascar; the Cimbicidae are entirely northern except for some peculiar genera in South America; the Megalodontidae are entirely palaearctic.

Facile explanations of these peculiar distributions are not now justified. Enough, however, has been said to show that, whereas some European groups of sawflies are entirely northern in distribution, others appear to have relationships with present tropical faunas.

5. VARIATION, PARTHENOGENESIS AND INTRA-SPECIFIC CATEGORIES

(*a*) Polymorphisms

(i) **Polymorphic larvae**

There are numerous instances of differently coloured larvae giving rise to adults scarcely distinguishable or not distinguished from each other. [By larvae is meant feeding larvae as distinct from

prepupae (last instar larvae) in which related species often assume a common colouring.] In most of these cases the habits of the larvae are quite different, e.g. solitary in *Diprion similis* Htg., gregarious in *D. pini* L.; or on different foodplants, e.g. *Croesus septentrionalis* L. on various trees including *Alnus* and *Betula*, *C. varus* Vill. always on *Alnus*, *C. latipes* Vill. always on *Betula*; or with a different distribution, e.g. the three forms of larvae called *Cimbex quadrimaculata* Müll: (1) S.E. Europe and Asia Minor; (2) Mediterranean region; and (3) Central Europe (Enslin).

In one or two species with a general green larval body colour occur rare "red larvae." These red mutants seem to be recessive to the normal and correlated with some constitutional weakness. This was observed by Cameron in *Nematus* (*Pachynematus*) *clitellatus* Lep. (Tenthredinidae, Nematinae) but he found the red form delicate and difficult to rear. Several species of *Pristiphora* related to *ruficornis* have a green larva with a more or less white to red anal region; occasionally I have found entirely red larvae of this group in Hertfordshire, but they too were delicate and I could not rear them. As recorded by Cameron, Brischke found reddish or yellow-ochre larvae of the normally bluish green *Cimbex lutea* L. (Cimbicidae). These likewise were very difficult to rear and ejected more blood from their pores when handled. Brischke bred both males and females from this red larva. More recently, red larvae have been found in *Gilpinia polytoma* Htg. (Diprionidae). The normal larva here is green with five longitudinal white stripes, but a form with a salmon-red venter occurs occasionally, though only in males, and it is found to be recessive to the normal form and to appear only in the fourth instar larva (Smith 1940). This appeared in Czechoslovakian stock, but Sellers (1942) records it also in Finland and Sweden. In the latter country a second red type of larva also occurs: "salmon red in colour throughout with a greenish tinge." In the fifth instar the red venter became "dirty yellow-red tinged with green."

In *Cephalcia campestris* Fall. (Pamphiliidae) 10 to 12 % of the larvae are recorded by Enslin as having in Central Europe a yellow instead of a green body-colour.

In several *Tenthredopsis* species yellowish-brown as well as green forms of the larvae occur.

(ii) **Sexual dimorphism**

Many of the sexual dimorphisms are clearly functional and connected with enabling the males to compete for the females, or to find them or hold them. Such characters are the enlarged eyes of most males compared to their females (grotesquely so in the Cimbicid Abiinae) and greater development of many other sense

organs such as antennae (which are usually longer and often more ciliate or branched in males); more powerful jaws (notably in the Cimbicid Cimbicinae); stronger wings (in a few British species the females are more or less flightless, e.g. the Dolerine *Dolerus anthracinus* Klug and the Nematine *Amauronematus abnormis* Holmgren and *Pristiphora coactula* Ruthe; flightless females also occur in *Dolerus oertzeni* Konow (Greece), *D. ciliatus* Konow (S. Russia), in the Nematine *Nematus* (*Euura*) *abortivus* MacGill. (Alaska) and in the entirely wingless female of the Blennocampine *Cacosyndia dimorpha* Freymouth (of Samarkand)); enlarged hind legs and tarsal claws (e.g. *Macrophya* and other Tenthredininae and the Nematine *Croesus* as well as many Cimbicidae, etc.).

The peculiar male hind wings with a marginal vein occur in various genera of Tenthridininae (e.g. *Tenthredopsis*, *Perineura* and *Sciapteryx*, and also in a few other Tenthredinid subfamilies (e.g. *Taxonus*, *Periclista* and *Caliroa* of Blennocampinae)). It is of unknown significance.

(iii) **Other polymorphisms**

A species may show great variation in adult colouring (e.g. females of *Tenthredopsis litterata* Geoffr., both sexes of *T. nassata* L. or some of the *Dolerus* species mentioned under "British Endemic Elements," 4 (*f*)) or in sculpture and wing length as in *Pristiphora coactula* Ruthe, and yet there is little doubt as to the species' limitations; but a supposed very variable "species" may consist of one variable species overlapping the colour range of several less variable species (Enslin, for example, included the morphologically distinct *Athalia cordata* Lep., *cornubiae* Benson, *liberta* Klug and *scutellariae* Cam. all within his interpretation of the very variably coloured *lineolata* Lep.).

We are therefore always in doubt as to whether a further analysis of any of our supposed very variable "species" may not reveal hidden species likewise. Where the polymorphism is clearly discontinuous (e.g. males of *Cladius*) we can only guess at the truth until the forms are studied genetically. If the polymorphism is confined to males, then it should be remembered that males, being haploid in chromosome number, might be expected to reveal various recessive mutants, while polymorphic females of a species may easily pass for a group of obligatory parthenogenetic species (see under "Parthenogenesis," 5 (*c*)).

In *Eutomostethus juncivorus* Rohw. (Japan), a species superficially very similar to our *E. luteiventris* Klug, occur two female colour forms showing in Okayama a seasonal dimorphism; the first brood, or those emerging in the spring (April to June) have a red mesonotum, while the second brood or those emerging in the

autumn (September to October) have a black mesonotum. Harukawa and Kondo (1930) found by experiment that this colour could be controlled by regulating the temperature at which the cocoons were kept. If kept at 15° C. all females developed into the spring form (red mesonotum), at 25° C. all females developed into the autumn form (black mesonotum), while at 20° C. the forms were mixed (4 spring and 13 autumn, with 17 intermediate). The mixture of forms at 20° does, however, suggest that a genetic factor was present also.

In British sawflies melanic elements are mostly correlated with the north and north-west (see under "British Endemic Elements," 4 (*f*)), but none of them have been correlated definitely with low temperature (high humidity would appear to be a more likely cause to judge, not only from distribution records, but also from comparison with other invertebrates (Wigglesworth 1939, Huxley 1942)). *Eutomostethus juncivorus* Rohw. thus has no close parallel with anything we know in Britain, but it is mentioned here as an example of the kind of factors that may be at work.

In the two British obligatory parthenogenetic species *Mesoneura opaca* F. (Nematinae) on *Quercus* and *Eutomostethus ephippium* Panz. (Blennocampinae) on Gramineae, we have rather similar colour variation, the former showing every intermediate between the two extremes (red and black mesonotum) and the latter dimorphic with very few intermediates. In the former of these species every population seems to show much the same range of variation (the proportions of the different variations have not been investigated), but in the latter although both forms can be found flying together in the south of England the dark form alone occurs in Scotland. Thus *E. ephippium* Panz. is represented in the British Museum by the following specimens:

England: 15 black form (2 partly red); 38 red form
Scotland: 8 black form (2 slightly red); 0 red form

Since both these species are obligatory parthenogenetic forms there is no chance for the interchange and recombination of genes as in *E. juncivorus* Rohwer. The variation of *Mesoneura opaca* F. seems to me very extraordinary, as one would have expected local segregations with different gene-combinations or some correlation with edaphic factors, especially as they are heavy slow-flying insects not likely to be dispersed by man or much by wind. The variation of this species, therefore, appears to offer an interesting field for special study.

The examples treated above mostly concern the well-known increase in the extent of black melanin pigments in insect body colours in the more humid climates. In many species or races there

is increasing paleness in pubescence, wing-membranes, wing-venation, apical leg-segments and in the yellow body colours with increasing cold; so that an arctic-paleness is characteristic of northern or mountain-top forms. It seems that this is very likely due in part to the known effect of cold on pterin pigments (cf. Wigglesworth 1939 and Hovanitz 1941).

(*b*) Chromosome Numbers

For most of the information given here about chromosome numbers I am indebted to Prof. A. D. Peacock of Dundee, either directly or through his various papers or those of his students Sanderson and Greenshields (1935) and Greenshields (1937).

The data for the Diprionidae are taken from Smith (1940). Normally, female sawflies are diploid in chromosome numbers and males haploid. The normal diploid number appears to be 16; the known exceptions are Cladiini of Tenthredinidae (*Cladius* and *Priophorus*) with 12, and *Pristiphora erichsoni* Htg. and *Strongylogaster macula* Kl. with 14 (Peacock and Sanderson 1939). In the Diprionidae the normal diploid number is 14, but *Gilpinia polytoma* Htg. has but 12 and *Diprion simile* Htg. 28.

The following is a complete list of all the chromosome numbers known in sawflies. Species marked with an asterisk * are not known to be British, but no information is available about species outside Europe.

Siricidae	*Urocerus gigas* L.: n=8
	Sirex cyaneus F.: n=8
Argidae	*Arge ustulata* L.: n=8
Cimbicidae	*Cimbex femorata* L.: n=8
	Trichiosoma lucorum L.: n=8
Diprionidae	*Diprion simile* Htg.: n=14
	**Gilpinia abieticola* D.T., *hercyniae* Htg., and *pallida* Kl.: n=7; **G. polytoma* Htg.: n=6
	**Macrodiprion nemoralis* Enslin: n=7
	Neodiprion sertifer Geoffroy: n=7
Tenthredinidae	Selandriinae
	Dolerus aeneus Htg.: n=8
	Aneugmenus stramineipes Kl.: n=8
	Strongylogaster macula Kl.: n=7
	S. mixta Kl.: n=8
	Blennocampinae
	Monsoma pulverata Retz.: n=8
	Nematinae
	Cladius pectinicornis Geoffr.: n=6
	Priophorus varipes Lep.: n=6
	Pristiphora erichsoni Htg.: n=7

Croesus septentrionalis L., and *varus* Villeret, *Nematinus luteus* Panz., *willigkiae* Stein and *fuscipennis* Lep., *Nematus* (*Pachynematus*) *obductus* Htg., *Nematus* (*Pontania*) *viminalis* L. and *pedunculi* Htg., *Nematus* (*Pteronidea*) *leucotrochus* Htg., *melanaspis* Htg., *nigricornis* Lep., *pavidus* Lep., *ribesii* Scop. and *viridescens* Cameron, *Nematus* (*N.*) *lucidus* Panzer, *Pristiphora pallipes* Lep. and *ruficornis* Olivier: n=8

(*c*) Parthenogenesis

(i) General

As hinted above, parthenogenesis will occur readily in most species of sawflies; in several, even common, species males are very rare or yet entirely unknown, at least in the northern parts of their range (see Section (δ) below), so that female-producing parthenogenesis (=obligatory or thelytokous parthenogenesis) is the normal role.

In most species parthenogenesis is facultative or arrhenotokous, that is to say giving rise only to male offspring (see Section (γ) below), but, in a few, males and females are produced and the parthenogenesis is spoken of as deuterotokous (see Section (β) below). In the facultative forms the sex of the offspring depends directly on whether the ova are fertilized, unimpregnated females producing entirely male offspring; by this simple mechanism there is a very nice balance set in the sex ratios. In the Nematine *Nematus* (*Pteronidea*) *ribesii* Scop. Kemner (1924) and Miles (1932) have studied the alternating sex cycles that seem to occur locally in natural populations. They explain this by saying that a generation in which males predominate would result in a greater number of fertilized eggs, and hence females in the next generation; and so males again in the one after. These oscillations about the normal sex-ratio are probably, however, affected by various other factors: (1) Females often start to oviposit without waiting for a male and soon after emerging. Any of the eggs laid before the females are impregnated by a male would, of course, be male; and it would appear that the proportion of males to females, even though males are very active and polygamous, would have to be excessive to prevent any infertile eggs being laid before copulation. (2) Different generations often overlap in their flight period. I have already referred to Miles's account (under "Larvae and General Biology," 3 (*b*)) of the confusion of generations that he found in *N. ribesii*, through some strains passing through three rapid generations a year while others, after a single generation, went into diapause till

the next spring and so on. In his account there were five different flight periods in a single summer; early males of one flight might easily find laggard females of a previous flight.

In the double-brooded strains of the Diprionid, *Neodiprion lecontei* Fitch in N. America, these alternating sex cycles have become stabilized into alternating generations of sexually reproducing and parthenogenetic forms. Rohwer (1915) says: "In the first generation mating is the rule while in the second it is exceptional. In localities where there is only one generation mating normally occurs and there is a preponderance of males; in localities where there are two or more generations mating occurs normally only during the first, but in such localities mating may be witnessed throughout most of the season because of the great overlapping of generations. There is no courtship in this species, and the females of the first generation take as active a part in finding a male as does the male while the females of the second generation will fight and may kill a male rather than mate." It is just possible, as in parallel cases, that *N. lecontei* really consists of a pair of species (normal and parthenogenetic) occurring at different seasons. Accepting the evidence at its face value, the results may be far-reaching, for we must consider the possibility that an alternation of sexual and parthenogenetic generations may occur elsewhere and cover some of our supposed cases of species pairs.

The effects of continuous obligatory or female-producing parthenogenesis appear to be of some practical and theoretical importance and will be further considered here. Where this form of parthenogenesis occurs in the sawflies, one would at first sight expect to find groups of closely related species, physiological, biological and local races, etc., because each individual in an entirely female-producing parthenogenetic race is the potential foundress of a new species perpetuating any harmless genetic mutation, for mutations must become homozygous and recombinations of genes are impossible. One would perhaps have expected to find large complexes of forms, comparable with the "clones" in vegetatively reproducing plants. In nature this does not appear to be so. Such local forms do not appear to be specially prevalent in obligatory sawflies. Even where rare males do occur, it is not clear that they can fertilize obligatory females to produce offspring that are not triploid. It is not known how obligatory and facultative races could hybridise and it would appear that when both occur in a taxonomic species, they must belong to physiologically isolated races, unless this type of parthenogenesis is brought about simply by crossing over a temperature threshold (see below) which could be recrossed by migration of individuals or changes in climate.

Against the tendency in obligatory species to produce pure-lines,

homozygous for any mutation, and the rapid increase of the number of individuals from unisexual reproduction, must be set the disadvantage they must suffer from, in lacking the interplay of selection on the recombinations of genes. As this is considered so important as to have favoured bisexual reproduction throughout most of the animal and plant kingdoms, its absence theoretically ought to be a real disadvantage and should greatly restrict variation by modified mutations. All mutations, it is presumed, would have to appear at once in homozygous form and, being generally deleterious at first, would be purged out by selection. Thus purged of their innate variability they are doomed to extinction with any major change of climate, as soon as survival comes to depend on a rapid adaptation to new conditions. At the same time this purging must be going on in all hymenopterous males, which are all believed to be normally haploid. It is not, however, very apparent that Hymenoptera have suffered any evolutionary handicap in this way; on the contrary they are one of the most successful and are the most numerous in species of all Insect orders. It would appear, therefore, that some compensating adjustment must exist.

The genetic difference in related obligatory (apomict) and facultative races of sawflies would be expected to lead to divergence into distinct forms through genetic isolation; but the divergence would presumably be lop-sided and mainly restricted to the race retaining normal sexual reproduction with its normal recombination and selection of genes. In support of this it is to be noticed that the obligatory species *Gilpinia hercyniae* has chromosome n=7, the normal number for the family, while the facultative *G. polytoma*, the supposed parent of *G. hercyniae*, has n=6, and has thus departed from the normal number of the family and in this respect is more specialized than its supposed daughter species!

This tendency for obligatory races to appear in the north is probably correlated with temperature as it has already been shown conversely in the laboratory that in *G. hercyniae* the proportion of rare males is increased as the temperature is increased (Smith 1940). We can thus visualize a normal sexually-reproducing strain in a warmer climate throwing off apomict strains along its northern fringe or in mountain ranges; several possible instances of this having happened can be seen below (Section (δ)). In some, no possible parent stock is now known, as, for example, for the closely related obligatory species *Nematus* (*Pontania*) *proximus* Lep., *bridgmannii* Cam., and *triandrae* Bens. In others it appears that the parent and apomict daughter species now overlap in Britain (e.g. *Dolerus nitens* Kl. and *D. possilensis* Cam.); and with this type of species proliferation it would not seem that geographical isolation is always necessary.

(ii) Types of parthenogenesis in European sawflies

Species marked with an asterisk are not known to be British. Many of the records are taken from Enslin p. 29; others are added from various sources.

(α) *Species known to have facultative or arrhenotokous (male-producing) races*

In some of these, e.g. *Cephus cinctus*, and *Nematus* (*Pteronidea*) *ribesii* and *Amauronematus puniceus* thelytokous (female-producing) races also exist.

Cephidae	*Cephus pygmaeus* L., **C. cinctus* Norton
Argidae	*Arge enodis* L., *ustulata* L., **berberidis* Schrank, *ochropus* Gmel.
Cimbicidae	*Trichiosoma lucorum* L., *Cimbex lutea* L. and *femorata* L., *Abia nitens* L.
Diprionidae	*Diprion pini* L., *Gilpinia frutetorum* F., *polytoma* Hartig. and **laricis* Jur. *Neodiprion sertifer* Fourcroy
Tenthredinidae	Selandriinae, *Dolerus aeneus* Htg., *Strongylogaster mixta* Kl., and *macula* Kl. Blennocampinae, *Ametastegia glabrata* Fall., *Athalia rosae* L., *Allantus cinctus* L., *truncatus* Kl. and **viennensis* Schrank, *Empria tridens* Konow.
	Nematinae, *Cladius pectinicornis* Geoffroy, *Priophorus varipes* Lep. and *Trichiocampus viminalis* Fall., *Amauronematus fallax* Lep., *puniceus* Christ., etc., *Croesus septentrionalis* L., *Nematinus abdominalis* F., *Platycampus luridiventris* Fall., *Pristiphora abietina* Christ., *conjugata* Dahlb., *geniculata* Htg., *ruficornis* Ol. and *testacea* Jur., *Nematus* (*Pteronidea*) *curtispina* Thoms., *hypoxanthus* Först, *melanaspis* Htg., *miliaris* Panz., *pavidus* Lep., *ribesii* Scop., *salicis* L., *viridescens* Cam. etc., and *Nematus* (*N.*) *coeruleocarpus* Htg. and *lucidus* Panz.

(β) *Species known to be sometimes deuterotokous (male- and female-producing)*

Cimbicidae	**Pseudoclavellaria amerinae* L. (Peacock 1938)

Tenthredinidae Nematinae
Priophorus tener Zadd. (Comrie 1938)
Hemichroa crocea Geoffr. (Cameron)
Nematus (*Pteronidea*) *polyspilus* Först. (Enslin)
N. (*Pt.*) *curtispina* Thomson (Cameron)
[In the N. American *Pikonema alaskensis* Rohw. Gobeil (1939) found no difference between the progeny of fertilized and unfertilized females, in both cases the proportions of males and females were approximately equal.]

(γ) *Species whose parthenogenetic offspring are sterile*

[Here can be included the N. American **Neodiprion burkei* Rohwer (Diprionidae) (Burke 1932).]

(δ) *Species known to be normally obligatory or thelytokous* (*female-producing*)

The following species are known to be obligatory, in at least part of their range, either through breeding experiments or (in common species) by the apparent extreme scarcity of males in the field. In those marked with † males occur in central or southern Europe, but have not been found in Britain. Where another species is enclosed in brackets this refers to a species in which males occur normally, which lives in proximity to the obligatory species although their full ranges may not coincide, and which is considered to be so closely related as possibly to have been derived from the same parent stock as the obligatory (apomict) species.

Cimbicidae *Cimbex connata* Schrank (*C. lutea* L.)
Abia candens Konow (*A. sericea* L.)
Zaraea fasciata L.

Diprionidae *Gilpinia hercyniae* Htg. (*G. polytoma* Htg.)

Tenthredinidae Tenthredininae, *Macrophya punctum-album* L.
Selandriinae
Dolerus possilensis Cameron (*D. nitens* Zaddach)
Aneugmenus coronatus Kl., *stramineipes* Kl., and *temporalis* C. G. Thomson
Blennocampinae
Eriocampa ovata L. (**E. umbratica* Kl.)
†*Eutomosthethus ephippium* Panz.
E. luteiventris Kl.
Rhadinoceraea gracilicornis Konow
†*Halidamia affinis* Fallén
Monophadnoides confusa Konow (*M. waldheimi* Gimm.)
Monophadnus pallescens Gmel.

Monostegia abdominalis F.
†*Monsoma pulverata* Retz.
Protemphytus pallipes Spinola
Caliroa cerasi L.
Endelomyia aethiops F.
Fenella nigrita Westwood and **F. minuta* Thomson
Fenusa dohrni Tischb. (*F. pusilla* Lep.) and *F. ulmi* Sund.
Metallus gei Brischke (*M. pumilus* Klug)
Fenusella hortulana Kl. (**F. wüstnei*), *F. nana* Kl. and *F. glaucopis* Konow
Heterarthrinae, *Heterarthrus aceris* McLachl. (**H. wüstnei* Konow and **leucomelus* Kl.) and *H. nemoralis* Fallén
Nematinae
Amauronematus tunicatus Zadd.
Anoplonyx duplex Lep.
Pseudodineura fuscula Kl.
Croesus varus Vill. (*C. septentrionalis* L. or *latipes* Vill.)
Hemichroa crocea Geoffroy and *australis* Lep.
Mesoneura opaca F.
Nematinus willigkiae Stein (*N. luteus* Panz.)
Pristiphora abbreviata Htg. (*P. monogyniae* Htg.), *P. pallidiventris* Fallén (*P. denudata* Knw.), *P. erichsoni* Htg. and *P. pallipes* Lep.
Nematus (*Pachynematus*) *obductus* Htg. and *P. vagus* F.
Nematus (*Pontania*) *bridgmanii* Cameron, *proximus* Lep. and *triandrae* Benson
Nematus (*Pteronidea*) *viridescens* Cameron, *P. polyspilus* Först. and *spiraeae* Zaddach

(*d*) Intraspecific Categories

(i) Foodplant races

The association today of a sawfly group with a group of closely related plants may indicate that the common ancestor of the sawfly group was associated with the common ancestor of the related plants. The Nematinae, for example, are associated mainly with the Rosaceae, Salicaceae, Betulaceae and Fagaceae, families considered by Hutchinson (1926) to be closely related phylogenetically. On the other hand, the association may be purely physiological, closely related plants being more similar physiologically. At the same time, in the Nematinae, there are a number of species or

groups of species associated with entirely different plant families. Where it is only an odd species the change over to a new foodplant may be very recent (e.g. *Pristiphora laricis* Hartig.); but where a whole group is concerned (e.g. the *abietina* group of *Pristiphora* on *Picea* and *Larix*) it may have been a common ancestor of the group that made the change.

Even species of sawfly with the most catholic taste in foodplants feed only on a very limited number of plant species; none are known to feed outside the Vascular Plants; and no species is known today that feeds on both coniferous and angiosperm plants, though some must have done so in the past, as closely related species of a genus today may feed one on a conifer and the other on an angiosperm (e.g. *Pristiphora laricis* Hartig on *Larix* and *P. pallipes* Lep. on *Ribes*). Likewise fern-feeding species are mostly restricted to ferns, either as individual species or as whole genera (many in the Selandriinae) or even as larger groups, including a whole family—Blasticotomidae.

In *Pristiphora quercus* Htg. (Nematinae) we find some feeding on *Betula* and others, not distinguished from these, feeding on *Vaccinium* spp.; they are not known to attack any other plants. Likewise the Nematine *Nematus* (*Pachynematus*) *vagus* F. is attached to *Salix* spp. and to *Carex* spp.; *Nematus* (*N.*) *crassus* Fallén to *Betula*, *Salix* or *Populus* on the one hand, and *Rumex obtusifolius* L. on the other; and *N. coeruleocarpus* Htg. to *Salix*, *Populus* and also several Ranunculaceae. How specialized each race (or group of races) is to each foodplant (or group of foodplants) is not known, but, by comparison with other Nematinae, it would appear that the herbaceous races were derived recently from the arborescent, as the Nematinae as a whole are attached to arborescent angiosperms.

These different intraspecific races of *Pristiphora quercus* and *Nematus* are probably at least potentially distinct species and in these, as in many similar cases, we can see the way in which have come about numerous species-pairs attached to distinct plants; or, taking it a step further, we find related pairs of genera or pairs of subfamilies with different hostplant preferences, as can be seen by reference to the Systematic Paper.

The generally narrow restriction of a sawfly species to a few related foodplants, for example in *Pristiphora*, is offset by the wide range of choice shown by the composite foodplants of all the sawflies in the genus, including knots of species on Coniferae and Ranunculaceae as well as Rosaceae, Salicaceae, Betulaceae, Corylaceae, Fagaceae and Grossulariaceae.

In *Dolerus* are four main species groups, two of them attached to *Equisetum* (Filicales) and the other two to monocotyledonous angiosperms, one to Juncaceae and the other to Cyperaceae and

Gramineae. In *Tenthredo* there are common species such as *T. mesomelas* L. showing a wide range of foodplants covering several different families; *T. ferruginea* Schrank and *T. livida* L. which combine this with great variation of colour pattern; and the *T. atra* L. complex in which a variable and polyphagous common species acts as a cloak for a number of rare forms of unknown status, some such as *T. monialata* Klug (restricted to *Menyanthes trifoliata* L.) being generally treated as a distinct species; the genus also contains a great many rare isolated species that vary little in habit or form.

It is impossible that all the sawflies could have evolved in step with the plants concerned, because, as I have already mentioned, there occur odd species of a pair or groups of species that have bridged the gap between groups such as Coniferae and angiosperms or angiosperms and Filicales, groups that did not evolve contemporaneously.

The impression gained thus in the study of sawfly foodplants is that periods of foodplant instability have alternated during the evolution of a group with periods of stability, that polyphagy is neither more primitive nor more advanced than monophagy, each being characteristic of a different stage in a recurring evolutionary cycle. In group after group there is evidence of an earlier burst of foodplant instability that has left its impress in the form of isolated knots of closely related species on a restricted group of foodplants, isolated from a similar knot on another restricted group of plants.

The idea of spontaneous recurring cycles of different types of variation was suggested by Warren (1937) in his studies of the genus *Erebia*, and something like this seems to me to be the only possible explanation. A burst of physiological variation leading to vigour, abundance and spread of the species is followed by a burst of morphological variation; this again is followed by retrenchment, selection by the environment and so segregation of different forms, which by the splitting up of the species in its range into isolated pockets become geographical races, and so new species. A revival of the cycle of variation is no doubt restricted to certain lines while others become static and decadent.

The environment does not enter into Warren's theory, but the most favourable conditions for speciation would surely lie in the interplay between these cycles of variation and the cycles of geographical and climatic changes during an unstable period.

One factor affecting a choice of foodplant during a period of instability may well be pressure from parasites. For parasites often seem more attached to a micro-ecological community than to any one species member of it (cf. Cushman 1926) and by starting out on a new foodplant in a new micro-ecological niche, the host may get

the better of its parasites for a time. Then ecological association appears to be another of the factors, presumably combined with some physical or chemical similarity. Thus the rosaceous hostplants of *Priophorus varipes* Lep. (Cladiinii) all agree in containing the glucoside amygdalin. In the butterflies the presence of mustard oil seems to be the essential character of all the foodplants of our Common Whites, *Pieris brassicae* and *rapae*; the larvae will attack any leaves, and even starch or paper, on which mustard oil has been smeared (cf. Wigglesworth 1939).

This aspect of the subject has scarcely been investigated, but there is certainly evidence of rules underlying the foodplant ranges and new foodplant choices. There is, for example, the Nematine *Nematus* (*N.*) *coeruleocarpus* Htg. which attacks Salicaceae and also Ranunculaceae. This is not, however, the only Nematine attacking Ranunculaceae; we have the whole genus of leaf-mining Nematinae, *Pseudodineura*, and we have also *Pristiphora thalictri* Kriechb. and *fuscata* Benson (on *Thalictrum*) and *P. alnivora* Htg. (on *Aquilegia*), each with closely related species on Salicaceae and allied families. Now, although the majority of at least temperate sawflies are associated with arborescent hostplants, in group after group we find sections that have gone over to some herbaceous group of hostplants. Thus the close association in arborescent hostplants of Rosaceae with Salicaceae, Betulaceae and Fagaceae has a parallel among herbaceous hostplants in the association of Ranunculaceae with Monocotyledons. This is almost a complete picture of the hostplants of the Blennocampinae! Both these associations show a remarkable correlation with Hutchinson's views (1926) on the phylogeny of flowering plants. First of all he postulates a dual phylogeny with distinct arborescent and herbaceous lines. In the arborescent he relates the Salicaceae, Betulaceae and Fagaceae by deriving them from rosaceous ancestors; in the herbaceous he derives Monocotyledons from Ranunculaceae, thus again relating them! These relationships no doubt have also a biochemical correlation which for the sawflies is more important than the mere historical.

On the whole the leaf-mining, leaf-edge-rolling and especially gall-making species have the closest physiological intimacy with their foodplants, and have the most restricted foodplant ranges of all. When we come, for instance to the leaf-mining Heterarthrinae and Fenusini of Blennocampinae and Pseudodineura (Nematinae), we find the species are limited to, at most, a single plant-genus and would appear now to have sacrificed most of their plasticity. Even in the Fenusini we find two, not yet distinguished, races of *Fenella nigrita* Westwood, one on *Agrimonia eupatoria* L. and the other on *Potentilla reptans* L.

The closest intimacy of all seems to be in the gall-making *Nematus* (*Pontania*), in which the foodplant range is limited to individual species or species-groups of *Salix*. Carleton (1938) managed to induce *Nematus* (*Pontania*) *proximus* Lep. (from *Salix fragilis* L.) to oviposit on *S. triandra* L. and *N. triandrae* Benson (from *S. triandra*) to oviposit on *S. fragilis*, but, from the very few malformed galls resulting, not a single fertile offspring was she able to breed.

Harrison (1927), in his well-known experiments with *Nematus* (*Pontania*) *viminalis* L. (=*salicis* Christ.), likewise found difficulty in getting individuals bred from galls on "*Salix Andersoniana* Smith" to oviposit on *S. rubra* Hudson (=*viminalis* L.×*purpurea* L.) in a reserve where no *S. andersoniana* existed; but he claimed that after one or two seasons a strain of this species had become established on *S. rubra*, and that this new host preference had become germinally fixed.

Thorpe (1930 and 1931) has already pointed out that this Lamarkian conclusion is not essential in interpreting the facts, and that the tendency to select for ovipositing the foodplant on which the insect fed as a larva might result from physiological responses.

There is still more that must now be said about these experiments. It should be remarked that the species selected for these experiments belongs to a very critical group taxonomically, not yet at all completely explored, and that several other species of the complex are already known to occur in the area where the experiments were conducted (cf. Harrison 1937); these include, for example, *N. harrisoni* Benson 1940 (on *Salix purpurea* L., and other species including *S. rubra*) not known at the time of the experiments, and there may well be still others not yet described. An alternative explanation of the facts, and no more hypothetical, could be that the original strain failed to establish itself on *S. rubra*, but that some other species came in and succeeded in establishing itself there. It is therefore now essential that some of the original stock of adults on *Salix andersoniana* should be compared with some of the strain later found on *S. rubra* in the light of recent taxonomy. But, whatever the result of this comparison, until the experiments have been successfully repeated, with some technique to prevent any possible infiltration, any conclusions drawn from them remain hypothetical.

(ii) **Other kinds of races**

Various other kinds of races seem to exist in which foodplant preferences are not the main isolating features.

The numerous cases where sibling species occur together on the same plant (e.g. *Nematinus* on *Alnus*, *Nematus* (*Pteronidea*) many

groups on *Salix*, etc.) indicate that the origin of such diversity was not the foodplant differences here. Several cases of these are discussed under "Parthenogenesis," 6 (*e*). There are also those races with present-day geographical isolation as the main feature, and Mayr (1942) argues convincingly that geographical isolation is normally one of the essential stages passed through in speciation; some of these are discussed under "Origin of Biogeographical Types," 4 (*e*).

There are others in which the temperature optimum or threshold of development differs. Harukawa and Kondo (1930), for example, found two strains of the Blennocampine *Eutomostethus juncivorus* Rohwer at Okayama and Hyögo in Japan (two localities at the same latitude though Hyögo is 90 miles further east). The Hyögo strain had three broods a year compared with the two of the Okayama strain and in the spring emerged almost 27 days earlier, having a lower temperature threshold of development (see also discussion under "Polymorphism," 6 (*c*)).

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